Psychological Monographs

Binocular and Monocular Relations in Foveal Dark Adaptation

BY

C. A. UNIVERSITY

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I

INTRODUCTION

The investigation described in the following pages deals with
" dark adaptation," or the increase in retinal sensitivity to abso-
lute brightness that occurs during a period of removal of all light
stimulation. It had for its specific aim the discovery of the
presence or absence of " binocular summation," that is, of greater
binocular than monocular retinal sensitivity when monocular and
binocular absolute brightness thresholds are compared during the
course of dark adaptation. In attacking the problem it was
necessary to take account of the discovery during the last quarter
century of a sharp distinction between the type of adaptation in
the fovea, or spot of clearest daylight vision, and that in the
extrafoveal retina. The difference is so great that most investi-
gators prefer an explanation in terms of the " Duplicity " theory.
Foveal adaptation is supposed to be a function of the cones only,
while extrafoveal adaptation, at least after the first few minutes
of darkness, is attributed to the rods. It seemed imperative,
therefore, to avoid the confusion of foveal and extrafoveal
adaptation which has rendered most of the earlier comparisons
of monocular and binocular thresholds difficult to interpret and,
in some cases, valueless.

Since lack of time prevented a thorough investigation of
binocular summation for all parts of the retina, the existence or
non-existence of foveal summation was alone studied. The
results of all previous experiments on summation in which any
regional differentiation was made apply to the extrafoveal retina.
Further, all previous comparisons of monocular and binocular
foveal thresholds were begun only after presumably maximal
dark adaptation of the fovea. A more adequate and accurate
comparison is secured by taking left eye, right eye, and binocular
thresholds at intervals from the beginning of dark adaptation to
the cessation of increase in foveal sensitivity. This procedure,

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used in the investigation here described, has the additional advantage of yielding data on the temporal course of dark adaptation. As the experimental work proceeded it became feasible to take monocular thresholds after either monocular or binocular light adaptation. We were thus able to compare the effect of binocular and monocular light adaptation respectively on succeeding monocular thresholds.

The main body of the monograph deals in order with history, apparatus and procedure, report of experimental data, and theory. The historical section is abridged from a more extended discussion in the author's doctoral dissertation on file in the Yale University Library. How great a rôle apparatus plays in the solution of our problem may be seen from the fact that the chief reason for delay in the discovery of the unique character of foveal adaptation, and for the paucity of studies on foveal binocular summation, has been technical difficulties in apparatus construction. First among such difficulties is control of foveal fixation. In our experiment fixation was controlled by the use of four luminous spots lying just within the margin of a visual field bounded by an artificial pupil. Since a very slight movement causes one of these spots to darken or disappear, fixation could be corrected at once by a compensatory eye movement in the opposite direction.

Light adaptation was induced by means of strong light reflected from screens located within the main part of the apparatus, and so situated and controlled that the subject, having once assumed his position, did not have to change it at all in order to give his judgments when, on cessation of light adaptation, the threshold stimulus was exposed. Thresholds could therefore be determined within a few seconds after the lights inducing light adaptation were extinguished. Accurate timing of the rapid change in foveal sensitivity (decreasing thresholds) during the first few seconds of dark adaptation was obtained by the use of smoked drum and electric markers in circuit with switches controlling the light adaptation lights and with a reaction key near the subject's hand. The above and other features of the apparatus will be described in detail. Calibration of the stimulus

and light adaptation lights will be discussed in the photometric
section.

Altogether 9 subjects were used. More than two-thirds of
the experimental work was done with 2 of these, the author
(Subject T) and his wife (Subject D). The two acted alter-
nately as experimenter and subject. It was possible, with these
two subjects, to make a thorough comparison of binocular and
monocular thresholds during the rapid increase in sensitivity
occurring in the first thirty seconds of foveal dark adaptation,
and to take a sufficient number of measurements after 30 seconds
in darkness to make the results statistically reliable. The author
feels justified in asserting, therefore, that the data showing 50
per cent lower binocular than monocular thresholds afford con-
vincing evidence of that degree of foveal binocular summation
for these two subjects. Similar considerations apply to their
results on the form of the foveal dark adaptation curve and the
influence of binocular light adaptation on succeeding monocular
thresholds. The methods by which the possibility of an " error
of expectation " was eliminated and other variables controlled
can best be understood from the later detailed description of
procedure.

Because of lack of time only relatively little work could be
done with the other 7 subjects, and although these experiments
afford valuable data, they do not justify conclusions of the same
degree of finality as does the more intensive work with (D) and
(T). In general, the most striking feature of the data from
these 7 subjects is individual variability, both in occurrence and
degree of foveal summation. Such variability is in keeping with
results of previous investigators on extrafoveal summation.

During the last part of the experiment, results from 3 subjects
opened up a new line of investigation, which, as far as it could
be followed, gave evidence of 2 types of foveal adaptation. The
results on this point are presented and their relation to a some-
what similar discovery of Abney and Watson discussed. Then
follows a comparison, by analysis of data given previously, of
the effects of 1 and 3 minutes light adaptation on succeeding

dark adaptation. A short summary of the main results completes the section on experimental data.

The final section of the monograph deals with theory. The bearing of our results on the conclusions of other investigators in regard to the form of the foveal dark adaptation curve, to binocular summation, and to the effect on monocular thresholds of stimulation of the other eye are presented. The author hopes that the discussion of the foveal dark adaptation curve may aid in clarifying what has been largely a dispute about words. On the other two topics no novel theories are offered, but a number of hypotheses of previous investigators are discussed in the light of our results. Some suggestions are made toward a possible reconciliation of apparently conflicting experimental data, and on the most desirable direction for future experimental work.

II

HISTORICAL

The historical background of the present investigation is represented in the literature * by reports on four more or less distinct problems.

A. General dark adaptation. The first experiments concerned this problem. The distinguishing feature is that the stimuli subtended large visual angles, so that both foveal and extrafoveal retaina were stimulated.

B. Foveal dark adaptation.

C. Binocular summation.

D. Influence of stimulation of one eye on the thresholds of the other.

A. *General Dark Adaptation*

Early investigators of the increasing sensitivity of the retina during a stay in darkness took little account of regional differences in sensitivity. It is therefore not surprising that their only important finding that has been substantiated by later research is Piper's discovery of the enormous increase in parafoveal retinal sensitivity during dark adaptation. This increase in sensitivity, measured by the ratio of the intensity of an initial threshold stimulus to one taken after longer dark adaptation, Piper found to vary from 2,000 to 10,000 times in different individuals, after a dark adaptation period of 1 hour. Succeeding work has shown that the increase is even greater than Piper supposed. Hecht (23) found a rapid increase in retinal sensitivity during the first 30 seconds of dark adaptation (not tested by Piper), and Achmatov (2) ascertained that after 24 hours of dark adaptation the intensity of the threshold stimulus fell to one-fifth of the

* A bibliography of previous work on dark adaptation is appended. For summaries see Tschermak (57), Roelofs and Zeeman (45), Hecht (23, 24), and the author's doctoral dissertation on file in the Yale University Library.

intensity required at the end of the one hour period. The other major conclusion of Piper, that the rate of adaptation is slow for 15 minutes, faster for the succeeding 30 minutes, and then slow again, has been shown by Hecht to be due to the former's method of plotting the curve of retinal sensitivity from the reciprocals of the threshold intensities. Hecht has shown (23) that when the threshold intensities are plotted against the time of dark adaptation the drop is at first rapid and slows up thereafter.

B. *Foveal Dark Adaptation*

Foveal dark adaptation is much more difficult to study than extrafoveal. There are several reasons for this. In the first place the foveal area is small. Parsons (37) gives the area of the fovea proper as 0.24 to 0.3 sq. mm. (55′ to 70′ visual angle), while the rod-free area averages about 0.8 sq. mm. (3° 3′ visual angle). Further, perfect fixation cannot be maintained, especially in darkness. Head and eye movements cause gross errors unless carefully controlled, and can never be entirely eliminated even under the best conditions. Thirdly, after a few minutes in darkness (for most subjects) the sensitivity of the parafoveal retina exceeds that of the fovea, and the difference becomes more and more pronounced the longer dark adaptation continues.

Considering these difficulties, it is not surprising that early investigators disagreed. Charpentier (57), the first to find a foveal sensitivity increase in darkness, was opposed by Parinaud (57), who argued for a complete lack of central dark adaptation. The resulting controversy, in which Fick (21), Trietel (54), and Von Kries (30) also took part, was not settled until 1904, when Nagel and Schaeffer first systematically attacked the problem (36). They were quite conscious of the difficulties and combined three methods in an attempt to overcome them:

(1) Use of a fixation point.

(2) Testing with extreme reds as stimuli.

(3) Taking thresholds in the first few minutes of dark adaptation.

The first, as Nagel points out, involves the possibility of dis-

turbance of dark adaptation. The second has the advantage that the periphery is much less sensitive to extreme reds than other colors. The third applies only to the first few minutes and fails to test the last part of the curve. Results for a 1° stimulus showed a drop in 10 minutes to about one-fourth the stimulus intensity necessary at the beginning. Tests with blue, green, and violet gave similar results, though there was great variability and fixation was difficult to maintain.

Wölfflin (60) improved procedure by using artificial light adaptation. His results are somewhat similar to those of Nagel and Schaeffer for a ½° or 1° stimulus. He reports a slow increase in sensitivity for 20 minutes, varying in its ratio of beginning to end points from 10 to 55 times in different individuals. For a 2° stimulus, however, the retinal sensitivity had increased 400 to 600 times at the end of half an hour. The work of Inouye and Oinuma (28) and of Dittler and Koike (19) has been reviewed by Hecht and need not be treated at length here. The comparison of brightness method used was novel and ingenious, and though criticized by Hecht (24) has considerable value. In general the findings support those of Wölfflin for a 1° stimulus, showing an increase in sensitivity of 14 to 25 times during a half hour stay in darkness.

The most ambitious attempt to determine the curve of foveal dark adaptation has been made by Hecht (24). He mentions three errors in preceding work: (1) Little control of intensity and time-periods of previous light adaptation. (2) Change from light adaptation to dark adaptation not clean cut and accurately timed. (3) Disturbance of dark adaptation by taking thresholds temporally close together. All three errors he carefully controlled.

For light adaptation he set up a white linen screen (in a dark room) illuminated from behind by two 150 W. lamps. Immediately above the screen was a long black box projecting from the subject, containing the threshold-stimulus mechanism. This consisted of a piece of opal glass (55 cm. from the subject) in front of which was placed a Wratten filter No. 70, which allows transmission only of rays beyond 650 $\mu\mu$ (extreme red). The

stimulus area was defined by a cross-shaped hole, 24 mm. in
diameter, in a piece of cardboard immediately in front of the
filter.   The stimulus light was on a movable track and the
stimulus intensity for each position of the lamp was calculated by
the inverse square law.

Thirty minutes of dark adaptation preceded the actual experi-
ment.   The subject then sat in the chair with his gaze directed
at the linen screen and the adaptation light was turned on.   At
the end of 5 minutes the light was turned off, the subject raised
his head, looked in the box, and announced when he saw the red
cross.   Observation was monocular and thresholds were taken
alternately with each eye for 20 minutes, when the subject was
light adapted again and the procedure repeated.   Fifteen sub-
jects were used and 2 sets of 10 determinations (10 points in the
dark adaptation curve) were taken, one set for each eye.

The results show a very rapid drop in threshold intensities for
the first 30 seconds, followed by a much slower drop to the end
of the 20 minute period.   There is continuous negative accelera-
tion and the composite curve is very smooth.   The gross drop
between 7 sec. and 30 sec. dark adaptation is from 40 x 10 ml.
to 12 x 10 ml.   That is, the threshold intensity at 30 sec. is
30 per cent of the threshold at 7 sec.   Seven seconds was the first
point accurately measured.   At the end of 20 min. the liminal
value has reached 3.4 x 10 ml.   The data are due to two factors—
change in the size of the pupil and dark adaptation.   Corrected
for Reeves' pupillary measurements, the 40 at 7 sec. remains
constant, 12 becomes 15, and 3.4 becomes 5.5.   The true dark
adaptation threshold at the end of 20 min. is thus 15 per cent of
the threshold intensity 7 sec. after light adaptation had ended.

Workmanlike as his procedure is, Hecht's experiment suffers
from a defect so serious as to make it doubtful whether he was
testing foveal vision alone.   Consider the method of observa-
tion.   The subject merely "looks into the viewing box."   There
is no attempt to hold the head steady or to provide an adequate
fixation device.   With his procedure there is no reason why the
stimulus should be picked up first by the fovea.   The subject is
merely looking (in total darkness) somewhere in the general

direction of the stimulus. Moreover, the rod free area is very small, averaging about 3° visual angle. Hecht's stimulus subtended an angle of 2.5°, so that, even if the eye were oriented properly, the slightest shift would throw the stimulus in whole or part on a parafoveal region of the retina.

The most probable explanation of the constancy of Hecht's results lies in the quality of the stimulus. It is well known that the sensitivity of parafoveal regions (at least to 10°) for extreme red is very close to that of the fovea. The work of Abney and Watson*(1) and Kohlrausch*(29) is conclusive on this point. Since the filter used by Hecht limits the transmission to the rays beyond 650 $\mu\mu$, it would make little difference in the results on what part of the foveal-parafoveal retina the stimulus fell. He was testing, not foveal dark adaptation, but adaptation for extreme red of a large portion of the retina.

Somewhat before this time Abney and Watson (1) had tested the relation of foveal and parafoveal brightness sensitivity in light adaptation, and also after the retina was " thoroughly dark adapted." During light adaptation the foveal and parafoveal (2.5°) thresholds were approximately equal down to 500 $\mu\mu$ (spectral lights). For a wave length of 493 $\mu\mu$ the ratio of parafoveal to foveal brightness was 1.45 to 1, while for 457 $\mu\mu$ the ratio became 1.51 to 1. In the " thoroughly dark adapted eye " the results fall into two groups—corresponding to two classes of observers found by these investigators. For Class II, who possess approximately equal foveal and parafoveal sensitivity in dark adaptation, the ratio between these two is not far from that of the light adapted eye. The parafoveal-foveal brightness ratio begins at slightly over unity at the red end of the spectrum and mounts to 1.94 : 1 at the violet. Quite different are the results for Class I, who represent 80 per cent of the individuals tested. For these the parafoveal-foveal ratio begins at 1.14 : 1 at 685 $\mu\mu$ and reaches 27 : 1 at 430 $\mu\mu$. For both classes of observers the parafoveal image is very little brighter than the foveal for the most extreme red tested, 685 $\mu\mu$. Since the ratio drops with increasing wave-length, and Hecht had used rays from 650 to

* Described below.

the red end of the spectrum, it is highly probable that his stimulus
had approximately equal brightness value at any point on the
retina on which the stimulus happened to fall.

Some support for this, as well as other data on foveal dark
adaptation, we find in the work of Kohlrausch (29) on parafoveal
and foveal dark adaptation for colors. This investigator used
a 1/20° red fixation point and a 1° circular colored stimulus at
the fovea and at 1.5°, 5°, and 10° from it. The stimulus was
interrupted rhythmically by a pendulum swinging at such a period
that the stimulus was visible 1 second and shut off the next.
After 10 seconds light adaptation on a field having a brightness
of 5500 lux, the subject fixated the red point and the stimulus
was adjusted continuously from a slightly over-threshold value
to a point where the fading and reappearing glimmer was just
visible. Tests were made with yellowish white, red, orange,
green and blue. The results show a foveal adaptation for all
colors, rapid at first but then slowing down and reaching approxi-
mate constancy at 10–15 minutes. Parafoveally with all colors
there is the same initial quick drop and flattening out, but most
colors show sooner or later another sharp downward bend in the
curve. The time before the appearance of the second bend
increases with the period of prior light adaptation, and decreases
with distance from the periphery and the ratio of the parafoveal
dark adaptation threshold to the foveal light adaptation threshold.
Most important here, however, is its dependence on wave length.
Lights of long wave length show the second bend in decreasing
measure, while for " Red I " (730–685 $\mu\mu$) it does not appear
at all. The parafoveal curve has the same form as the foveal.

Kohlrausch's article, like many others, lacks important details.
No curves are given and the method of plotting is uncertain. It
would also be desirable to know the number of subjects, the time
elapsing after light adaptation before the first limen was taken,
the interval between readings, whether the red fixation point was
used in obtaining foveal thresholds, and whether the subject or
some one else made the adjustments. Objection might also be
made that the light adaptation time (10 sec.) was too short, that

there was no artificial pupil, and that the threshold light disturbed adaptation.

These objections, however, apply only to the absolute form of the dark adaptation curve. The investigation seems sound on two important points:

(1) Comparison of foveal and parafoveal dark adaptation.

(2) Comparison of dark adaptation for lights of different wave-length.

SUMMARY

The one important undisputed result of early studies of the course of dark adaptation is Piper's discovery of the enormous increase in extrafoveal retinal sensitivity in darkness; and investigation by Hecht of the first few seconds of dark adaptation and Achmatov over a 24 hour period has extended both ends of the dark adaptation curve and shown that the total extrafoveal sensitivity range in darkness is much greater than the 2,000 to 10,000 times increase in 1 hour found in Piper's subjects.

Technical difficulties, particularly in regard to visual fixation, retarded the study of regional differences in retinal adaptation to such an extent that the discovery of foveal adaptation came relatively late. In fact, its existence was not established until the investigation by Nagel and Schaeffer in 1904. The results of this and more recent work may be summarized.

1. The typical course of foveal dark adaptation is radically different from extrafoveal. If the stimulus intensities are plotted against the length of time of dark adaptation, both foveal and extrafoveal curves show a sharp initial drop succeeded by a relatively slow descent. The extrafoveal curve, however, has a later drop not found in the foveal. The range of sensitivity increase at the fovea is thus small compared with the extrafoveal increase given above. Estimates of the range of foveal adaptation vary from 4 (Nagel) to 55 (some of Wölfflin's subjects). The major part, perhaps all, of this variation is due to individual differences in subjects, and in intensity and duration of preceding light adaptation.

The duration of foveal dark adaptation is also sharply con-

trasted with extrafoveal. For almost all subjects tested, **foveal** adaptation ends in 10 to 30 minutes.

The general differentiation between foveal and **extrafoveal** dark adaptation has two exceptions noted below.

2. For **extreme red** the extrafoveal dark adaptation curve has the same form as the typical foveal curve for red and all other colors. There is no second drop in the curve and the total sensitivity increase is small.

3. For 3 of their 8 observers, Abney and Watson found practically equal foveal and parafoveal sensitivity after 30 minutes dark adaptation. Both fovea and parafovea showed typical extrafoveal results: high thresholds for extreme red, very low thresholds for violet, and intermediate values for other colors.

Although the foregoing conclusions are stated in somewhat dogmatic fashion, it would be unwise to infer that no further experimental work is needed. We have seen that earlier investigators failed to differentiate between foveal and extrafoveal sensitivity, and that few of those who later investigated presumably foveal dark adaptation thought it worth while to make comparative studies of other parts of the retina. To get an adequate picture of the dark adaptation of the retina unambiguously foveal and extrafoveal data are necessary, and the work of Kohlrausch points the way to what must eventually be carried out: an extensive investigation of both extrafoveal and foveal dark adaptation for a large number of subjects under identical or closely comparable conditions.

C. *Binocular " Summation "*

The problem here is that of the monocular-binocular relationship. Do the two eyes, as a rule, combine in the perception of brightness, or do they act separately? If the latter is true, we should expect the resulting binocular sensation to approximate that of the better eye. On the other hand, there is not definite agreement regarding what to expect if the eyes support each other in binocular vision. Piper (**40**), who first worked in this field, believed that the true binocular threshold is one-half the monocular. Laird (**31**) seems to feel that proof of complete

addition is necessary to demonstrate summation. In view of the general findings in the field, especially on account of the fact that rarely if ever does a given set of data show exact binocular "stimulus addition," the term "summation" will be applied in this paper to any results in which the binocular threshold is significantly lower than that for either eye.

Binocular-monocular brightness relations have been worked out in three fields:

(1) Flicker thresholds.
(2) Brightness thresholds.
(3) Supra-threshold brightnesses.

Of these the second only needs extended discussion. Summation of super-threshold brightnesses has been practically disproved. The only important positive findings, by Piper (41), have been analyzed and shown to be due to other factors by Roelofs and Zeeman (45). Piper had his subjects make judgments on two fields, one seen monocularly and the other binocularly. Roelofs and Zeeman, however, showed that during the monocular observation (presumably half the time) the nonobserving eye was dark-adapting, since the coördinate eye movements caused it to look directly at a black partition wall.

Sherrington (46), who performed the only important experiment on flicker summation, obtained negative results. The relation between dark adaptation flicker and brightness thresholds, however, is not well enough understood to permit any convincing evidence from Sherrington's work either for or against brightness summation.

The early work on binocular brightness summation has been reviewed by Roelofs and Zeeman (45) and need only briefly be referred to here. Piper (40), the first investigator, found no lower monocular sensitivity for the first 15 minutes. After this, however, the monocular and binocular curves diverged rapidly, until at the end of an hour the binocular sensitivity was approximately double that of either eye. Following Piper, Feilchenfeld and Loeser (22), Stargadt (31), Horn (27), Streiff (32), and Behr (10) did some work on the problem. Their results in

general supported Piper, although they found great individual variability. Some of Stargardt's and Behr's subjects, in particular, perceived threshold brightness as well monocularly as binocularly. Wölfflin's work, on the other hand, gives little support to Piper's conclusions. Most of his subjects had no greater binocular than monocular sensitivity. Lohmann (32, 33), again, found lower binocular thresholds in most cases, though the binocular advantage seldom approached complete summation.

Later, Roelofs and Zeeman (45), using only one subject, found approximately complete summation from the beginning of dark adaptation. Zeeman (61) again took up the problem, and his results show a somewhat lower binocular than monocular threshold. In no case, however, did the binocular threshold fall to half the monocular. A recent attempt at the solution of the problem has been made by E. Müller. His findings show little, if any, summation. An equal number of the lowest binocular limens lie above and below the corresponding values for the more sensitive eye. The variation in individual values is very great, especially on the descending threshold. Müller himself says that his results " die Frage nicht abschliessend lösen."

The question of the existence of binocular summation is therefore still unsettled. Moreover, none of the investigators attempted to isolate foveal from parafoveal summation. All used large stimulus surfaces. Piper, indeed, believed that binocular summation was a function of the rods only, and not of the cones. Since there are no rods at the retinal center he denied the existence of foveal summation. Neither he nor his successors, however, made any attempt to test his hypothesis directly. Piper's single reason for denying foveal summation was the fact that he found extrafoveal summation only after fifteen minutes of dark adaptation. At that time, he supposed, the rod mechanism had displaced the cones.

The only serious attempt to test foveal brightness summation has been made by Abney and Watson (1) for spectral colors. These investigators used a stimulus disc of about half a degree— well within the fovea. The first limens were taken after a 30 minute adaptation period. The stimulation was momentary and

descending thresholds only were taken. The subject put on the stimulus light, then if the light seemed above threshold he turned it off, lowered the intensity and tried again. This he repeated until the threshold was reached. Three sittings were taken for each wave-length used. The results show no summation for the two observers tested, either at the fovea or 5° distant. Where there was a difference between the curves for the right and left eye the binocular curve corresponded to the better one. Abney's results show remarkable constancy once the initial practice period was passed, and this must be taken as a strong factor in favor of their reliability, though it is difficult to understand how parafoveal thresholds taken in successive readings can be compared for different parts of the spectrum. Adaptation at the fovea (for Class I of his observers) seems to be practically over in twenty minutes, but extrafoveal adaptation goes on for hours and would be expected to vitiate his comparisons.

SUMMARY

The question whether binocular thresholds during dark adaptation are lower than those for either eye has thus received conflicting answers. Most experiments were merely incidental to other work, suffered from lack of thoroughness, and involved the use of large stimuli, thus failing to differentiate between the foveal and extrafoveal regions of the retina. The only serious attempt to test foveal summation, that of Abney and Watson, for 2 observers after 30 minutes of dark adaptation, yielded the result that the binocular curves corresponded to those for the better eye. There has been no investigation of the existence or non-existence of foveal summation during the temporal course of dark adaptation.

It would seem that the greater part of the work on summation remains to be done. Most pressing is the question of foveal summation, and particularly during the first 30 seconds after light adaptation, since for most observers the most rapid increase in foveal sensitivity occurs during the first 30 seconds of dark adaptation.

D. *The Effect of Stimulation of One Eye on the Dark Adaptation of the Other*

As in many other dark adaptation investigations, the first thorough work was done by Piper*(41). For dark adaptation he covered one eye with a bandage, while the other eye was kept constantly light adapted by fixating a white cardboard illuminated by an arc lamp. Every 5 or 6 minutes the light adaptation lamp was turned off, the bandage taken from the dark adapting eye, and two thresholds then taken, one monocularly with the dark adapted eye, and the other binocularly. The bandage was then replaced, the light adaptation light turned on, and the procedure repeated. The results show no disturbance of dark adaptation in one eye by stimulation of the other. The curve of increase of sensitivity is the same as that obtained when both eyes are dark adapted and thresholds determined monocularly.

The next work on the influencing of one eye by the simultaneous light stimulation of the other is that of Révész (44). He always dark adapted both eyes equally for 45 minutes or more before he took any thresholds. A binocular threshold was then taken followed by a monocular threshold with simultaneous light adaptation of the other eye. He came to the conclusion that the thresholds of one eye determined after dark adaptation did not vary in any regular way with the light stimuli influencing the other eye during the threshold determinations.

Such data seem to indicate that the condition of light or dark adaptation of one eye has no effect on the thresholds of the other. A careful analysis of the work of his predecessors, however, led Behr (10) to perform an experiment, the results of which appear to negate such an interpretation. He assumed that dark adaptation is dependent on the accumulation of visual purple, and argued that continuous light adaptation of one eye may prevent visual purple from accumulating in the other, but may not be able to destroy it when once accumulated. Révész by his preliminary dark adaptation period and Piper during his threshold determinations allowed some time to elapse during which both eyes could

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* Charpentier and Treitel made a few observations.

dark adapt in quite normal fashion. Accordingly Behr tested his hypothesis.

He constructed and set up before one eye a small lamp in a round opaque box open only on the side turned to the eye. On this open end was an adjustable diaphragm and behind the diaphragm a milk-glass plate to prevent undue glare and heat from reaching the eye. The box was fastened to the head in such a way that the head could move freely with it and the other eye dark adapt independently and be investigated without difficulty, the light in the box of the other eye being kept on continuously and the subject asked to keep the eye open.

Initial findings show an increase of sensitivity in the first minutes of dark adaptation in excess of Piper's curve. This he explains as due to his (Behr's) small amount of light adaptation. Further, there are no sharp bends in the dark adaptation curve. It approximates a straight line, and the sensitivity at the end of 45 minutes dark adaptation is cut to one-half of that which occurs with binocular dark adaptation and monocular threshold determinations. Another interesting point tested was the effect of simultaneous as compared with successive light adaptation of the non-observing eye. This was done by sometimes taking the monocular thresholds while the light was presented to the other eye, sometimes after it was turned off. Comparison of the two values shows no differences worth considering.

Results so far seem to indicate that beginning with both eyes equally light adapted:

(1) If both eyes are allowed to dark adapt for a certain (unknown) time, stimulation of one has no effect on the other.

(2) If one eye is kept continuously light adapted, the curve of increasing sensitivity of the other (dark adapted) eye is much straighter and at the end of 45 min. its sensitivity approximates half the normal.

In reality the matter is not quite so simple. Heymans (25), testing inhibition of a threshold ("passive") stimulus by simultaneous presentation of another ("active") stimulus, found that stimulation of one eye raised the threshold of the other in direct proportion to the intensity of the inhibiting illumination.

Heymans' work, which was done with only 1 subject, was repeated by Spencer (49) for 5 individuals. Stimulation was approximately foveal and the inhibiting intensities fairly low. The method of right and wrong cases was used. The results support the findings of Heymans. The average threshold when the highest inhibiting intensity is used was about double that of the uninhibited monocular threshold. As the author states, it is not certain whether this is a true inhibition or due to changes in dark adaptation of the other eye. The reflex contraction of one pupil when the other is stimulated might also account for some of the effect observed. Spencer and Cohen (50) further corroborated these findings in an extensive experiment with 1 subject.

In any case the results of Heymans and Spencer stand in contrast to those of Révész. The two investigations were carried out under closely similar conditions except that Révész had a somewhat longer preliminary dark adaptation period.

Some mention must be made of the work of Allen on the effects of various conditions of wave-length and intensity of stimulation on the critical frequency of flicker for different spectral colors. In his early experiments (3, 4) he studied the effect of intense pre-stimulation of one eye by different colors on the critical frequency of flicker in the same eye. The experiments were carried on in a dark room. Repetition of the work (5) in a well lighted room showed an " enhancement " of the whole spectrum. Since the eye used was light adapted in both cases by the intense stimulus light, the " enhancement " is interpreted to mean that the dark adaptation of the non-observing eye raised the flicker threshold of the observing eye. Comparison of curves for the " rested " eye under various conditions of daylight and darkness bears out such an interpretation. The close relationship found by Allen between pre-stimulation of one eye and the flicker threshold of the other has been mentioned before. For further data the reader is referred to an excellent summary and discussion by Parsons (38).

There are important differences between this work and any previously discussed. The difficulty of direct comparison of

flicker and brightness sensitivity has been stressed before. Also, in Allen's work the observing eye is continuously light adapted, while the data previously given concern the dark adapted eye. It is indeed impossible to test the effect of dark adaptation on the critical frequency of flicker alone. If the intensity needed at the beginning of the experiment is kept constant throughout, the process of dark adaptation is seriously disturbed by taking thresholds. On the other hand, if the intensity of the flickering light is lowered to avoid such disturbance, the data secured will be an unanalyzable resultant of brightness and flicker adaptation. The important point, however, is that Allen's remarkably constant results obtained by a carefully controlled method, show a reciprocal effect of stimulation of one eye on the thresholds of the other. In this they agree with Spencer and Behr and contradict Piper and Révész.

The question of the effect of stimulation of one eye on the brightness sensitivity of the other is therefore still unsettled. Moreover, there have been no experiments that attempted to differentiate between fovea and periphery. Spencer, who of previous experimenters used the smallest stimulus, secured only " approximately foveal vision."

III

Apparatus and Procedure

A survey of the literature on dark adaptation shows that the most pressing problem in this field is that of monocular and binocular relations during foveal dark adaptation. Although the question of the existence of extrafoveal summation has not yet been settled, it has been definitely worked over, while that of foveal summation has scarcely been touched.

It was therefore decided to attack the problem of foveal summation. To do this it was necessary to determine the course of foveal dark adaptation under comparable conditions for the left eye, right eye, and binocularly. The resulting data give both binocular and monocular relations and also a much needed check (with " white light ") on the validity of Hecht's curves of " foveal " dark adaptation for extreme red.

A. *Apparatus*

Construction of apparatus for our work proved a difficult task. A number of requirements had to be kept in mind:

(1) Control of intensity and quality of light adaptation.

(2) Quick transition from light adaptation to threshold-taking under dark adaptation.

(3) Adequate foveal fixation.

(4) Elimination of effects of pupillary changes.

(5) Accurate timing.

(6) Constancy of the threshold-stimulus source.

(7) Ease and convenience of manipulation and control.

While all these were carefully considered, the author claims special advantages for the apparatuus described in the following pages, in the neatness and dispatch of the light-dark adaptation shift, the accuracy of the timing, and the effectiveness of the fixation device. The first of these was secured by building the light adaptation screens within the main apparatus, so that the

experimenter could make the transition almost instantaneously by a movement that turned back the screens and simultaneously turned off the adaptation lights. This eliminated confusion and loss of orientation by the subject, since he kept his previously assumed position, and permitted threshold determinations almost immediately. Since accurate timing had been most difficult to secure during the rapid increase of sensitivity in the first few seconds of dark adaptation, a smoked drum and electric markers were used for timing thresholds taken during the first 30 seconds. The fixation device is something new in dark adaptation work and proved sensitive and accurate.

The main body of the apparatus consisted of a wooden box 5 ft. long and 6 in. x 6 in. inside measurement. The material was ½ in. white pine. Extending like wings from either side of the main box at right angles, and 7 in. from the front or viewing end, were two other compartments. These were of like material and shape to the main box, but were each 8.5 in. high instead of 6 in., and 2 ft. long instead of 5 ft. The bottom and sides were made light-tight by nailing, while the overlapping tops were fastened with screws and thus removable. The whole was painted dull black inside and out and mounted on a large table in a dark room.

Fig. 1, A, shows a horizontal section of the three boxes at the level of the eye. The long box, shown extending toward the top of the figure, we will call the " observation box." The side boxes will be named the left and right " light adaptation boxes." The observation box has three cross-partitions shown at (x), (y), and (w) in the diagram. The partition at (x) carries the artificial pupils, that at (y) the fixation " triangles," and the one at (w) the stimulus. A longitudinal partition extends from the (x) partition of the observation box to a point (z) about one foot from the subject's eyes. All partitions are the full height of the box and light-tight except for the openings mentioned later.

The arrangement for light adaptation needs more detailed description. The screens at which the subject looked were 2 sheets of milk-glass 5.75 in. x 6 in., hinged at one end and placed

Smoked
drum

Switchboard

a

b

c

d

E. Left light-
adaptation
screen

ⓢ

Motor
w

v   z

ⓑ   ⓢ

y

x
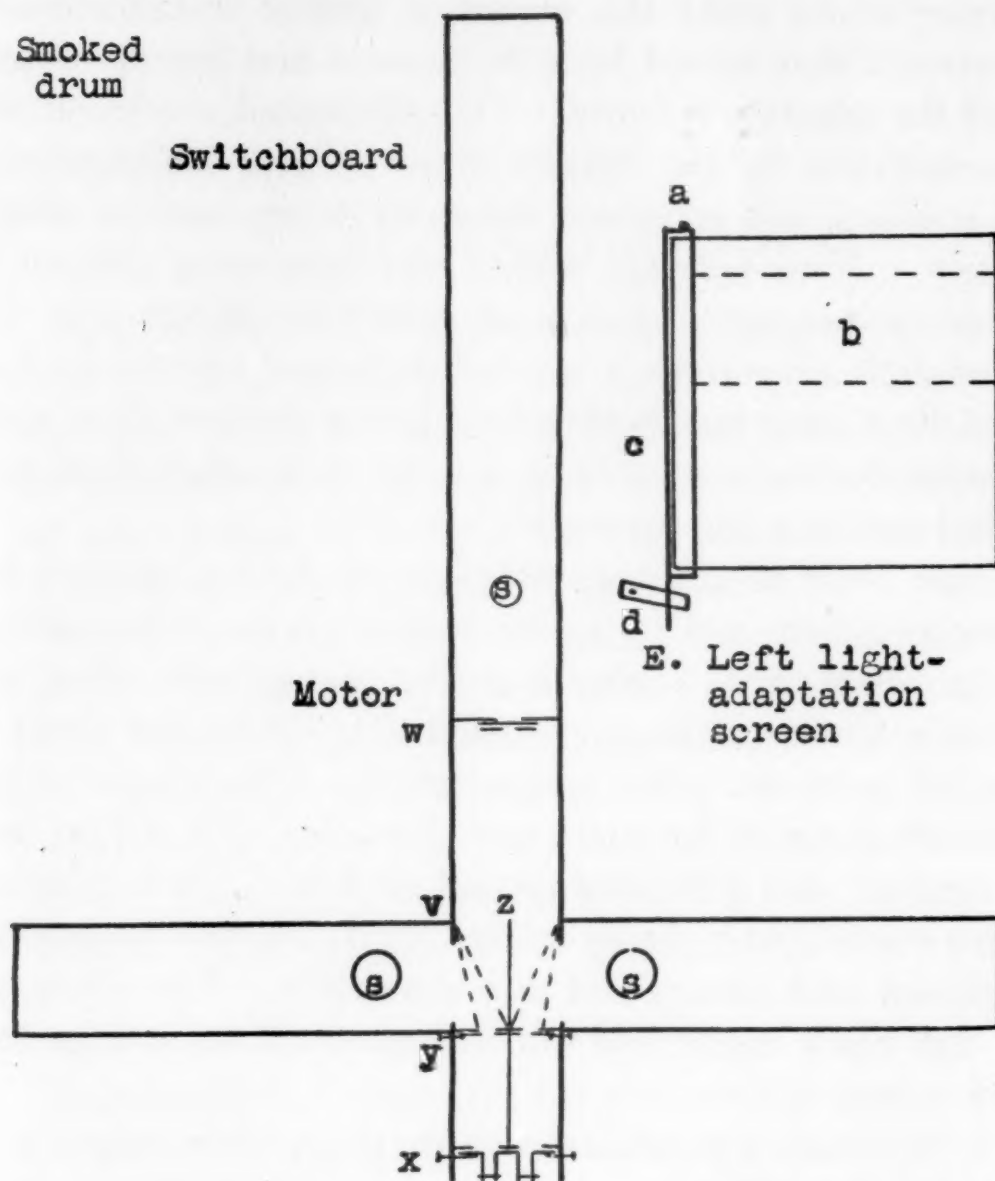
A. Horizontal section of main box at level of
   eye

p ○   ○ p

B. Left slide
on y partition
carrying fix-
ation points

C. Front view of cross
partition immediately in front of
subject (x).

D. Side view
of telescope
with artificial
pupil
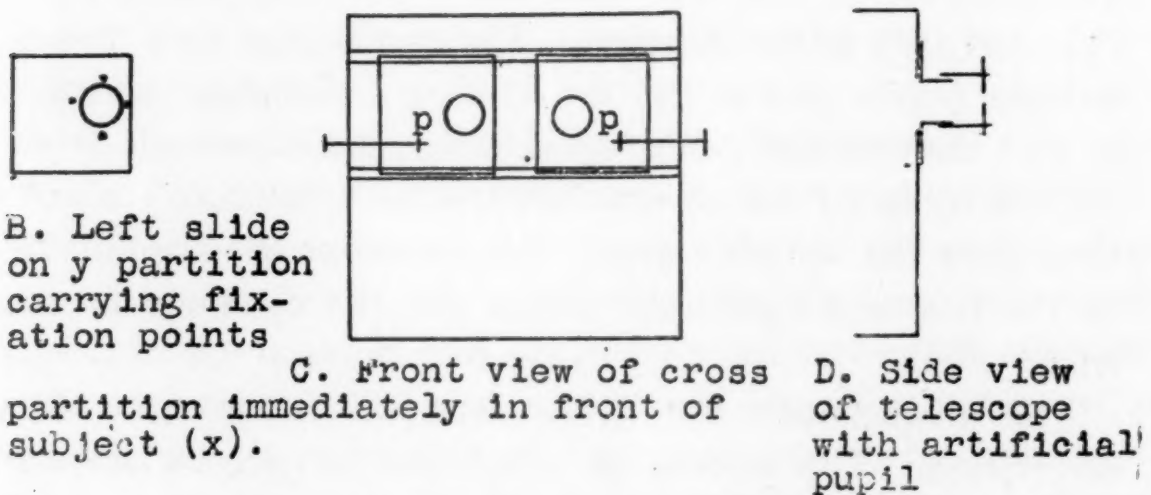
FIG. 1. Diagram of main body of apparatus.

vertically in the observation box directly opposite the light adaptation boxes. One side of each plate was painted dull black and the other side covered with a special black non-reflecting paper, except for a vertical strip 1.5 in. wide coated with magnesium oxide. The left light adaptation plate is shown at (E) in Fig. 1. The strip (b) coated with magnesium oxide is indicated by the dotted lines. At (a) are 2 narrow brass plates holding the milk-glass and soldered to the brass rod (c) which serves as a hinge. The light adaptation plates are placed vertically in the observation box in the positions showed by the dotted lines in Fig. 1, A. At (v) the brass rod on the left plate extends through holes in brass plates at the top and bottom of the box. The left plate is thus hinged door-fashion at (v) and swings like a door from one position to the other as shown by the dotted lines. The lines nearest the center of the observation box show the positions of the plates with the free ends against the central partition. This was the position for light adaptation, during which the plates were illuminated by light from lamps in the light adaptation boxes, reflected into the observer's eyes from the magnesium oxide surface of the plates. The outer dotted lines show the plates against the cross-partition and thus out of line with the subject's eyes. Thresholds were taken with the plates in the latter position.

The sources for light adaptation were 300 W. Mazda C blue daylight lamps operated on a 110 volt D.C. circuit. These lamps were mounted horizontally in the light adaptation boxes on sliding carriages, and the latter were adjusted so that the light falling on the magnesium oxide strip was 950 ft. candles.* The energy distribution per wave length for the two light adaptation lights was determined by the Electrical Testing Laboratories. According to the statements of illuminating engineers,† and a comparison of the curves for our lamps with those given by Parsons (37), the color of the blue "daylight" lamps is about intermediate between the yellowish-white of the ordinary tungsten lamp and sunlight. The original aim was to approximate sunlight as

* See photometric section.
† Letters from the Edison Lamp Works and Nela Research Laboratories.

closely as possible in order to duplicate normal light adaptation conditions. The only feasible method of doing this, however, was by use of the blue daylight filter put out by the Eastman Kodak Co., and since this filter has only 22 per cent transmission the resulting light intensity would have been too low for our purpose.

The switches which controlled the light adaptation lights also moved the light adaptation screens. This simultaneous movement was secured by means of lever arrangements connecting the left and right adaptation screens with the left and right adaptation switches, respectively. The light adaptation switches, which were placed at the point marked " switchboard " in Fig. 1, were spring wall-switches to which were fastened adjustable handles 4 in. long. One end of each lever arrangement was fastened to one of these handles, and the other end to one of the light adaptation screens (Fig. 1, E).

The same movement of the light adaptation switches that turned on the adaptation lights thus moved the screens in line with the subject's eyes, and the reverse motion of the switches put off the lights and moved the screens out of his line of vision. The left and right adaptation switches, though operating independently, were so placed that they could be moved together by one motion of the experimenter's hand.

As stimulus served a sheet of milk-glass in front of the opening in the cross-partition at (w) in Fig. 1, A. In front of the milk-glass and exactly in the center of the observation box was fastened an adjustable piece of thin tin having a circular hole 1 cm. in diameter. The hole, the edge of which defined the stimulus surface, was 24¼ in. from the subject's eye and thus subtended 55′ visual angle. The stimulus source was a Sharp-Millar photometer lamp mounted vertically on a movable carriage and accurately centered. Since the lamp has a very small filament and its nearest position to the milk-glass was 10 cm., it may be considered a point source for our purposes. The glass of these lamps is shaped to eliminate bulb reflection. They are also well " seasoned " at the Electrical Testing Laboratories before being sent out. Intensity was varied in fine gradations

by moving the stimulus lamp. Reading was done from a millimeter scale on the side of the track by means of a pointer illuminated by a faint red glow. For gross variations of intensity an episcotister was at first used. It was later found that the sudden increase of sensitivity during the first few seconds of dark adaptation made it only necessary to cut down the stimulus by one long step. Since preliminary work showed the most convenient single cut in intensity to be about 1/18, a neutral gelatine filter of 5.76 per cent transmission was procured from the Eastman Kodak Co.* The filter was inserted in front of the stimulus for all thresholds taken after 60 seconds dark adaptation, and the use of the episcotister discontinued. One subject, however, had so much lower absolute thresholds than the rest that the use of the filter had to be combined with one setting of the episcotister (90°). The episcotister was placed immediately behind the partition at (w) (Fig. 1, A) and driven by a silent spring phonograph motor at the position marked " motor " in the diagram.

Current for the stimulus lamp was supplied by two Edison storage cells. These delivered about 2.8 volts, which was cut down and kept constant at 1.57 volts by adjustment of two 20 ohm radio rheostats in series. Tests were made at the beginning and end and at frequent intervals throughout each session by putting a 3 volt Weston voltmeter in circuit across the lamp terminals. The Edison cells were so constant that current fluctuations throughout the experiment were negligible.

The diagrams in Fig. 1 also outline the fixation device. The main feature of this was based on a double use of artificial pupils. As is well known, artificial pupils usually function to control variations in the amount of light reaching the eye due to changes in the size of the natural pupil. In addition to control of stimulus intensity, however, the artificial pupil can be used to limit the size of the visual field. The possibility arose that changes in the margins of the visual field caused by eye movement under these conditions, might be used to control foveal fixation.

* The work on filters has been reviewed by Reeves (**43**). The Eastman neutral filters cause no appreciable color change.

Starting with this idea, a process of approximation and correction resulted in a device that gave satisfactory results.

Before further describing the fixation device, however, it is necessary to give some idea of the conditions imposed by use of artificial pupils in binocular vision. Since interocular distances vary, the distance between the artificial pupils must be adjustable. In our apparatus, sufficient adjustment was secured by mounting the pupils on 2 x 2¼ in. brass plates on the face of the partition (x) in Fig. 1, A). A front view of this arrangement is shown at (C) in the same figure. The plates (p) slid in grooves made by fastening narrow brass plates by screws to the wooden partition, and were adjusted by thumb screws turning in nuts soldered on the plates. On the face of each plate was also soldered a sliding tube arrangement carrying one of the artificial pupils. A side view of one of these " telescopes " is shown at (D) in Fig. 1. Each consisted of a short piece of thin brass pipe ⅞ in. in diameter, open at both ends. Over the inner pipe slid a similar piece of pipe just large enough to move easily with moderate pressure. Near the front end of the latter, slits were cut at the top and bottom, and through these was a piece of spring brass about ⅝ in. wide. A hole in the center of the brass strip served as an artificial pupil. The pupil, shown on the extreme right of (D), is necessarily exaggerated in the diagram. Actually it was bored by a No. 55 drill and lightly reamed out before and after painting. It is thus only .05 in. in diameter—slightly over a millimeter. Since the spring brass, though bent to hold firmly against the edges of the slits, was adjustable vertically, the artificial pupils could be adjusted in three ways: horizontally for interocular distance by right or left movement of the brass plates, toward or away from the subject by means of the " telescopes," and vertically by movement of the brass strips mentioned above. To permit clear view of the stimulus ¼ in. holes were cut in the brass plates and larger holes behind these in the (x) partition. Slides were placed in front of the artificial pupils so that the subject could shut off the vision of either eye. In some experiments another slide was used behind the light

adaptation screens so that observation could be varied between right, left, and binocular without the subject's knowledge.

The second part of the fixation device was on the cross partition at (y). This partition looked exactly like the face view of the (x) partition at Fig. 1, C, except for the fixation triangles. There were, of course, no artificial pupils on the second plates. Since the light adaptation screens were on the side of the (y) partition away from the subject, the light adaptation surfaces were defined by the ¾ in. holes in the plates on the (y) partition. The size of these areas and measurements given later show that each light adaptation surface subtended $5\frac{1}{4}°$ visual angle, which seemed ample margin for a stimulus of 55'.

The left (y) plate is shown at (B) in Fig. 1. On this may be seen four fixation spots (" triangles ") of luminous paint on a black velvet background. Each triangle was ⅛ in. from the edge of the central hole. As noted previously, the four triangles combined with the artificial pupil to control fixation. The distance of the subject's eye from the artificial pupil was adjusted so that the visual field defined by the circular edge of the artificial pupil just included the inner points of the four fixation triangles. Then a very small eye movement caused changes in the number or relative brightness of the spots present in the field. Looking toward a slight spot caused it to flash out of sight, while the opposite side of the field at once became brighter as the base of that triangular spot came into the field. The device can be demonstrated very simply. Make a pinhole in a piece of paper, and while facing a window, bring the paper up to the eye until you can see the full width of the window through the pinhole while fixating the center. Then look sharply to right and left and note the change in the margins of the field. The effectiveness of the device for gross eye movements is striking. The points brighten and dim and flash in and out of the field as the eye is moved back and forth. The smallest eye movement that gave a clearly perceptible brightness change for unpracticed subjects was ¾°. Since the rod-free area is about 3° and the stimulus only 55', detection of a 1° movement is sufficient. This practiced subjects could do easily.

For effective use of the fixation control just outlined, head movements must be practically eliminated. This was secured by a curved forehead rest padded with felt and tooth rests made from two wooden tongue-depressors cut down to four inches in length, fastened together, and held firmly by thumb screws in slots cut in two heavy brass pieces on the sides of the observation box. Biting on the tooth rest prevented vertical and side to side movement, while the forehead rest kept the subject's head from moving forward. Subjects W, H, and N used wax impressions on the tooth rests. Use of wax impressions almost entirely eliminated danger of fixation loss through head movements and also aided the subjects in getting reset before each threshold. They did, however, add to the difficulty of the initial adjustment. For this reason and because other subjects did not seem to need it, the additional precaution was not taken with them.

The distances from the subject's eyes to parts of the apparatus were thus:

Surface of cornea to artificial pupil	1.83 in.
Artificial pupil to fixation triangles	6.37 in.
Eye to stimulus	24.25 in.

Troland's formulas (56) show that the maximum stimulus diameter under the above conditions is .84 in. The 1 cm. stimulus used was thus well below any danger of variation in the amount of light reaching the retina due to changes in the size of the natural pupil.

The extreme sensitivity of the fixation control made the "lining up" of the stimulus, fixation triangles, and artificial pupils with the subject's eyes an arduous task. This was partly simplified by the fact that the vertical adjustment could be made for each subject by moving the brass piece holding the tooth rest. The artificial pupils were thus lined up vertically once for all by the experimenter, who also adjusted the "telescopes" so that each eye saw an equal amount of the triangles. Each subject made the horizontal adjustments to the proper interocular distance by turning the thumb screw to move the brass plates at (x) and (y). Each eye was set separately and the whole tested binocularly. The first setting was thus a lengthy process of

approximation and correction. After the first session the position of each adjustable part was read by the experimenter from millimeter scales attached to the apparatus, and for succeeding trials reset at the same points. Lining up by the use of the fixation triangles, however, proved a more sensitive method, and the subjects often had to make slight corrections of the experimenter's adjustments. The stimulus light was on at a fairly high intensity during the whole process of adjustment, and the subject fixated the center of the stimulus while balancing the fixation triangles.

As the self-light emanating from the luminous points proved insufficient for controlling fixation, it had to be supplemented. This was done by a No. 1142 Mazda 12–16 v. automobile lamp in circuit with 8 Edison storage cells. The lamp was mounted horizontally below the center of the observation box at (y) in Fig. 1. Two mirrors placed at suitable angles reflected the light from the source to the black velvet-covered plates holding the right and left fixation triangles. The light source and mirrors were inclosed in a small light-tight box. Two radio rheostats were used to cut down the current to the required amperage. Current constancy was tested by a Weston ammeter. The lowest intensities of the light that gave clear cut fixation control were determined empirically by approximation and correction of current strength. It was found that 2 intensities were needed, one at 1 amp. for thresholds taken during the first 30 sec., and a second setting at 0.8 amp. for all succeeding thresholds. Only the two intensities were used for all subjects with one exception. It might be thought that the light reflected from the fixation triangles and the surrounding surface would interfere with dark adaptation. While this is possible, several considerations made it probable that the interference would be negligible.

(1) The light fell only on the triangles and the black velvet background. The latter reflected little light and could only be distinguished from the deep black of the 3/4 in. central hole after 10 to 20 min. dark adaptation.

(2) The fixation triangles never fell on the fovea. Moving

the eye to focus one centrally caused it to disappear within the margin of the artificial pupil.

In any case the above objection would apply only to the absolute curve of foveal dark adaptation. Comparative work is not affected.

The artificial pupil as thus used, besides giving an excellent fixation control, has the subsidiary advantages of ensuring accurate centering of the artificial and natural pupils and making the distance from the artificial pupils to the eyes the same for all subjects.

Timing the course of dark adaptation during the first 30 sec. was done by electric markers on a smoked drum driven by a silent spring phonograph motor. These were mounted on a table at the position shown in Fig. 1. Current for the marker was supplied by 3 dry cells. The circuit, which also included a faint red signal lamp, could be closed by any of 3 parallel leads: 2 to the light adaptation switches and 1 to a reaction key near the subject's hand. As the light adaptation switch was turned off the moving handle momentarily closed the electric marker circuit and thus gave a record of the end of light adaptation. Pressing the reaction key by the subject when he secured his threshold also momentarily closed the marker circuit. The dark adaptation time preceding the threshold determination thus corresponded to the distance between the two records on the drum and was read from a seconds line made by another electric marker in circuit with the laboratory time clock. Gross times were taken by two stop watches having a lever arrangement operated by the experimenter's foot. The watches were so set that starting one stopped the other. The latter was then read and reset.

Readings and records were made with a small flashlight bulb supplied by 2 dry cells. The reading lamp and stop watches were enclosed in a box open only on the side nearest the experimenter. The light was operated by a switch and kept just bright enough for reading and recording by adjusting a rheostat in circuit. To further minimize the possibility of any stray light reaching the subject a large black screen was erected at (y) in

Fig. 1. A metronome for regulating the subject's winking during light adaptation completed the apparatus.

B. *Procedure*

The general conduct of the experiment was as follows: After the preliminary adjustments had been made the subject sat back comfortably in his chair for 15 or 20 min. dark adaptation. The fixation points were then faintly illuminated, the subject told to " get set." As soon as the flashing of the red signal lamp indicated that the subject had signified his readiness by pressing the reaction key, the light adaptation light was put on and the subject fixated the center of the bright surface for a 1 min. or 3 min. period. Five seconds before the end of the light adaptation period the experimenter turned on the light that illuminated the fixation points and also closed the stimulus switch and started the motor attached to the smoked drum. Exactly at the end of the period (1 or 3 min.) the light adaptation lights were turned off by a movement that also pushed back the screens and made the first mark on the drum. The subject, as soon as the light adaptation light went off, picked up the four fixation points and held fixation of these until the stimulus appeared. He indicated this appearance by pressing the reaction key, held the stimulus an instant to check up on fixation, and then sat back (in darkness) until called on again. For any threshold taken during the first sec. of dark adaptation the stimulus lamp was fixed at a predetermined position. For all thresholds taken after 30 sec. of dark adaptation the stimulus intensity was at first well below the threshold and the lamp moved towards the subject. Stop watches instead of the drum were used for timing and the stimulus switch was closed and the lamp moved up immediately after the subject had given the ready signal. Then on the flashing of the signal light that indicated the subject's perception of the stimulus, the experimenter stopped moving the lamp, read the stop watches and lamp position and reset these for the next threshold.

The instructions to the subject were made as simple as was feasible, and given at suitable times throughout the experiment.

First the function of the reaction key and the method of adjustment of head rest and slides on the (x) and (y) partitions were explained. The subject was next seated in the chair before the apparatus and told to look through one artificial pupil. The other artificial pupil was shut off by a slide. The subject was then asked: " Do you see the four bright triangles? Your head rest must be adjusted so that when you are looking straight at the circular disc in the center (the stimulus) the brightness of the four is evenly balanced and only the points visible." During the succeeding process of adjustment the experimenter checked up the subject's progress by frequent questions. Each eye was set separately and the whole afterwards tested binocularly. The experimenter could then verify and if necessary correct the centering of the stimulus for each eye.

The subject was now asked: "Are you set correctly? Now look sharply at one of the points. What happens to it? What happens to the one opposite? " When the subject by repeated trials had become familiar with the brightness change or disappearance of one of the points, the instructions were continued. " These points are used to control central fixation. You are to hold the points evenly balanced and watch for the stimulus. If a point dims or disappears you correct by moving the eyes slightly away from it. If one grows brighter move the eyes a little toward it. Try this a few times."

The subject next sat back for the preliminary dark adaptation. Near the end of this period he was told: " You are to be light adapted for 1 (or 3) minutes. When I say ' get set,' take up the position for observation with the fixation points balanced. When you are ready press the reaction key. During light adaptation a metronome will be sounding. Hold the center of the light adaptation surface as well as possible, count the metronome strokes, and wink every 5th stroke. When the light adaptation light is turned off the fixation points will come up almost immediately. Holding them balanced as directed, watch for the stimulus and press the reaction key as soon as you are sure you see the disc. After pressing the key hold fixation an instant to

see if the stimulus remains the same. Then sit back." After each threshold the experimenter asked: " How was the fixation?"

The instructions were completely given only in the first session. The subject's remembrance of the method of holding fixation was checked up in all early sessions and his impression of the accuracy of fixation determined after every threshold. All the subjects except C and T had an extended period of preliminary practice and were thoroughly familiar with the process of adjustment and the use of the fixation scheme before the experiment.

C. *Photometry*

Before the actual experiment the illumination of the stimulus and light adaptation surfaces was photometrically determined. In this a comparison of brightness method was used. Standard lamps were secured and the judgments made (with two exceptions) by those who served as subjects in the main experiments.

(1) STIMULUS

The standard light source used in calibrating the stimulus was a Sharp-Millar photometer lamp similar to the stimulus lamp, mounted on a movable carriage in the open dark room. The carriage was in turn mounted on a track in such a position that it could be moved only directly toward or away from the standard surface. From the known candle power of the lamp (0.123 c.p. in the direction tested; voltage across the lamp terminals, 1.36), as determined by the Electrical Testing Laboratories, the intensity of illumination of the standard surface for any distance of the standard lamp could be calculated by the inverse square law.

The standard surface was a magnesium carbonate block about an inch in front of the circular stimulus surface, and so placed that it shut off a little less than half the latter from the eye. Part of the magnesium block was painted black, so that the remainder matched in shape the now visible part of the stimulus surface. The relation between the light sources is shown in Fig. 2, A. The light from the stimulus passes through the milk-glass straight to the subject's eye. Rays from the standard lamp come in from

the side and are reflected. The inside of the observation box in this region was covered with black velvet to minimize reflection.

Calibration was done separately for each of 4 positions of the
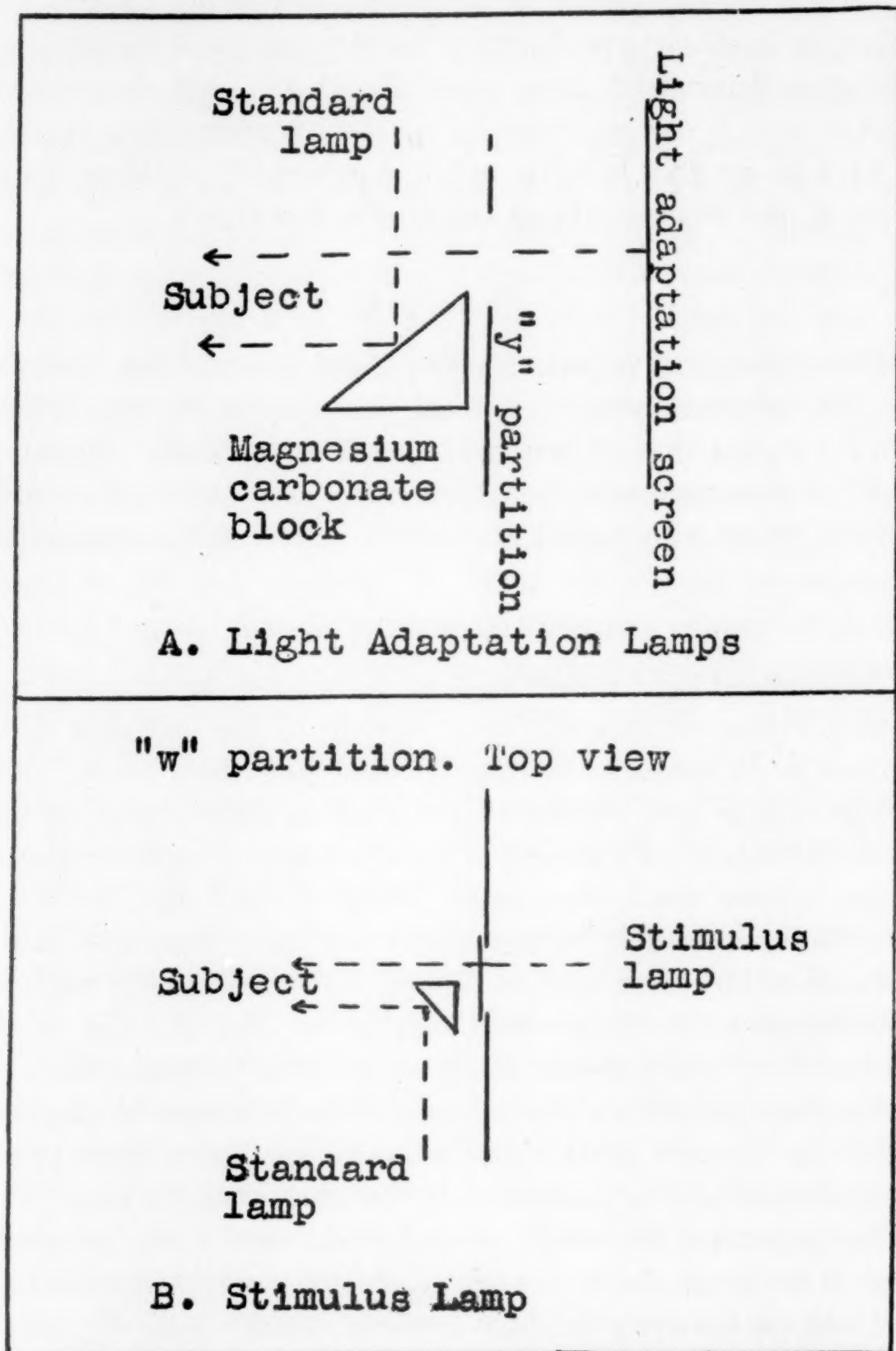
Fig. 2. Arrangement for Calibration of Light Adaptation and Stimulus Lamps.

stimulus light. These positions were 10, 20, 40, and 60 cm. distant from the milk-glass. Each of 7 subjects made 10 judgments of the point at which the brightness of the standard surface appeared equal to that of the stimulus surface. Both ascending and descending thresholds were taken. The averages of these 70 judgments are given below:

	Lamp position in centimeters.			
	10.00	20.00	40.00	60.00
Stimulus (fixed)	10.00	20.00	40.00	60.00
Standard (av. of 70)	15.85	30.36	58.50	84.59
Mean variation of standard	0.56	1.30	3.30	6.00

As the successive points did not lie in a straight line it was decided not to extrapolate for the lamp positions beyond 60 cm., but to take observations for one more position, 80 cm. Since 2 of the former subjects were not available the 80 cm. point represents an average of 50 judgments. Fortunately the subjects left out of this series were at the extremes. One gave the lowest and the other the highest judgments of the group, and the average of the two was close to the group average. Extending the curve in fact showed that the 80 cm. point lay directly in its path. The variability in each subject's judgments and between subjects was small.

In calculating intensity an arbitrary value of 10,000 light units was assigned to the position of the standard lamp 10 cm. from the magnesium block, and the illumination values for other distances of the standard lamp calculated by the inverse square law. The number of light units for any position of the stimulus light could then be computed from the corresponding position of the standard lamp.

The illumination of the stimulus surface in foot-candles may be calculated from the known candle power of the standard, namely, 0.123 c.p. This gives a surface intensity of 0.123 foot-candles when the standard lamp is 1 ft. from the carbonate block. The arbitrary value chosen: 10 cm. distance of standard lamp from surface=10,000 light units, is thus 1.14 foot-candles. The highest stimulus intensity (3,984 l.u.) equals 0.454 foot-candles.

When the experiment was about two-thirds completed both the stimulus and standard lamps were broken and had to be

replaced. The new standard lamp was rated at 0.133 candle power with 1.466 volts across the lamp terminals. Calibration of the second stimulus lamp was done by having each of 5 subjects (mentioned above) make 10 judgments of the standard with the stimulus at 20 cm. The average of the 50 judgments was the position 34.25 cm. (m.v. 0.5) on the standard lamp scale. This position formerly equaled 850 light units. But the new standard had 8.13 per cent more candle power than the old. The intensity at 34.25 cm. (standard lamp position) therefore now equals 850×108.13=919 light units. That is, at the 20 cm. position the new stimulus lamp gives a stimulus surface illumination of 919 light units. Now, the former calibration work shows that the old stimulus lamp gave a stimulus surface illumination of 1,084 l.u. at the 20 cm. position. It therefore follows that the intensity of the new stimulus lamp is 15 per cent less than the intensity of the old lamp. Accordingly all light unit values corresponding to the positions of the stimulus lamp had to be reduced 15 per cent in later calculations.

(2) LIGHT ADAPTATION

The standard lamp for calibration of the light adaptation lamps was a 500 W. Mazda C blue daylight lamp. This lamp was calibrated by the Westinghouse Lamp Company for foot-candles at two distances from the standard surface, at 110 and 100 volts. Their measurements are given below:

Volts	Distance from filament to reflecting surface	Intensity
110	12 in.	483 ft. candles
	6 in.	1863 ft. candles
100	12 in.	363 ft. candles
	6 in.	1390 ft. candles

In our work a 110 volt D.C. circuit was used. The standard lamp was mounted on an adjustable rod above the observation box immediately in front of the (y) partition. The light fell on a magnesium carbonate block in the observation box. The carbonate block was mounted on a wooden base covered with black velvet and so placed that the magnesium surface shut off the lower half of the light adaptation area from the subject.

These relationships are shown in Fig. 2, B. The diagram holds for either eye.

In the calibration work the standard lamp was fixed and the light adaptation lamps moved back and forth until they were judged equal to the standard. As with the stimulus both ascending and descending limens were taken. In setting the standard lamp it was found that neither the 12 nor the 6 in. distance from the magnesium block was suitable. The former gave too little intensity and in order to be equal to the latter the adaptation lights would have to be brought too near the inner end of the light adaptation boxes. Accordingly a position 8½ in. from filament to block was chosen. If the inverse square law held the intensity at 8½ in. would be midway between the intensity at 12 in. and 6 in. However, there is some deviation from the law. Half the intensity at 6 in.=931.5 foot-candles, and twice the intensity at 12 in.=966 foot-candles. Since the difference between these is less than 4 per cent, the average of the two gives a value for the 8½ in. distance well within the margin of error for this kind of work. The average is 948.75 or roughly 950 foot-candles.

Three subjects made 10 judgments apiece for each light. Their results were so consistent both within an individual's judgments and from individual to individual that this was considered sufficient. Averages for each subject are given below. The absolute numbers are arbitrary.

Subject	Lamp position (av. of 10)	
	Left	Right
A	5.30 in.	12.77 in.
N	5.30 in.	12.65 in.
H	5.27 in.	12.77 in.
av.	5.29 in.	12.73 in.

The adaptation lights were then fixed at the above points and so remained throughout the experiment.

IV

Experimental Data

As previously indicated, the results of our investigation are given in terms of brightness threshold intensities, taken monocularly and binocularly during foveal dark adaptation. The data throw light on the problem of foveal binocular summation; the effect of pre-stimulation of one eye on the sensitivity, in dark adaptation, of the other; and incidentally on the temporal course of foveal dark adaptation. The procedure also gave an opportunity to compare the effect of 1 min. and 3 min. prior light adaptation. In general, attention was paid to securing accurate comparative data. Such variables as fatigue or practice were equalized, as nearly as possible, for right, left, and binocular observation.

A. *Comparison of Right, Left, and Binocular Thresholds Taken During the First 30 Seconds of Dark Adaptation*

Since previous work indicated that a very large percentage of foveal dark adaptation takes place during the first 30 sec. in darkness, it seemed advisable to spend a large proportion of the time on this portion of the curve.* It was found, however, that securing accurate determinations so soon after light adaptation requires considerable practice and also seems to demand a different " mental set " from that of later observations. Indeed all threshold judgments made by unpracticed subjects during the first few seconds of dark adaptation showed great variability. It seemed best, therefore, to work intensively with 2 practiced subjects.

Each period of uninterrupted experimentation consisted of: (1) 15 min. preliminary dark adaptation. (2) 10 cycles of

* Barring the work of Hecht for extreme red light, only a few observations have been taken until after 30 seconds in darkness. No attempt has been made to get at binocular and monocular relations during this time.

1 min. light adaptation followed by 2 min. dark adaptation. One threshold judgment was made within 30 sec. after the end of each minute of light adaptation, the subject remaining in position until the stimulus appeared. An experimental period may be tabulated:

Adaptation	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
Minutes	15	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2

The primary reason for the shortness of the light and dark adaptation periods was to permit the taking of a large enough number of thresholds with the right, left, and binocular observation to bring out the true inter-relationships. The 1 min. light adaptation had the additional advantage of not fatiguing the eye muscles too greatly. Subjects found considerable difficulty in holding fixation for thresholds taken immediately after a 3 or 5 min. light adaptation period. The use of 5 stimulus intensities in a semi-random order served to eliminate the error of expectation.

In taking any one threshold the stimulus intensity was not varied. The stimulus lamp was set at a definite position before the end of the light adaptation period and was not moved until after light adaptation had ceased and the subject had signified his perception of the stimulus. The variable measured was the time between the end of light adaptation and the reaction of the subject. The stimulus intensity, however, was not the same for every threshold. In order to get enough points on the first part of the light adaptation curve five positions of the stimulus light were chosen. These positions corresponded to threshold intensities that an extended practice period showed were most likely to become visible within the first 30 sec. The five stimulus intensities were distributed in each experimental series in chance order, except for the following:

(1) Each of the 5 appeared twice in each series of 10 thresholds. This served to equalize the effect of practice and fatigue and day to day variability for each of the stimulus intensities.

(2) Each of the five appeared once and only once in each position of the series. The method of distribution of stimulus

intensities may be illustrated by the series of subject D at 2:30 P.M., Oct. 26, 1928.

| Adaptation | Time in minutes | —Right eye— | | Seconds before perception of stimulus |
		Lamp position	Stimulus intensity	
L	1			
D	2	28.3	560	9.2
L	1			
D	2	23.1	820	6.2
L	1			
D	2	40	300	17.2
L	1			
D	2	20	1080	5.4
L	1			
D	2	47.3	213	20.1
L	1			
D	2	23.1	820	6.3
L	1			
D	2	28.3	560	6.5
L	1			
D	2	40	300	17.1
L	1			
D	2	47.3	213	21.4
L	1			
D	2	20	1080	5.7

Here the intensity 28.3 (560 l.u.) is in first and seventh place. In the next session the same intensity occupied fourth and sixth place, and so on. This precaution was taken to equalize possible cumulative effects of the 10 successive light and dark adaptation periods, for each of the 5 stimulus intensities. It also had an additional advantage in that it gave an opportunity to find out whether any such effects were produced.

There were 4 variations of the monocular-binocular relationships:

(1) Right eye observation   Monocular light adaptation.
(2) Left   "   "   Monocular   "   "
(3) Binocular   "   Binocular   "   "
(4) Left eye   "   Binocular   "   "

For any one period of experimental work (15 min. pre-dark adaptation followed by 10 light and dark adaptation periods) only one of these variations was used. A sitting begun with the right eye observing was carried through with the right eye. Five repetitions of each of the four variations were made with

each subject. We thus obtained 10 thresholds with each stimulus intensity for each of the four monocular-binocular relationships. In only one instance did we fail to get 10 thresholds. The two highest intensities chosen for binocular observation with Subject D proved too bright and one much lower had to be substituted. The greatest binocular stimulus intensity for Subject D, 500 l.u., is therefore represented in our data by the average of 8 observations. The left eye curve after monocular light adaptation (2) was determined twice because the left eye curve after binocular light adaptation (4) was deter-
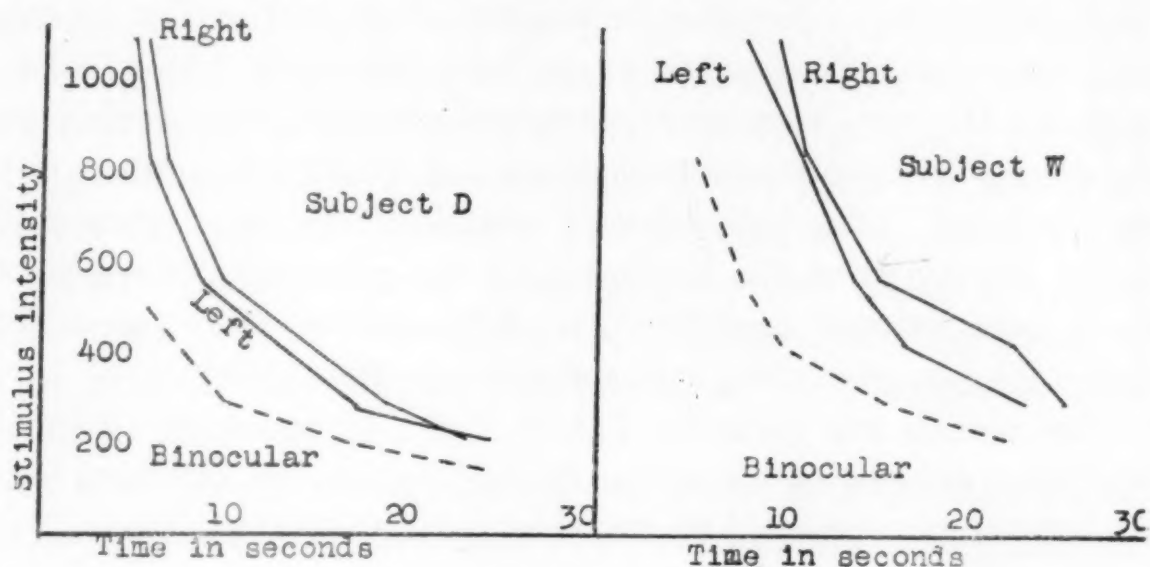
FIG. 3. Thresholds in 30 sec. Dark Adaptation.
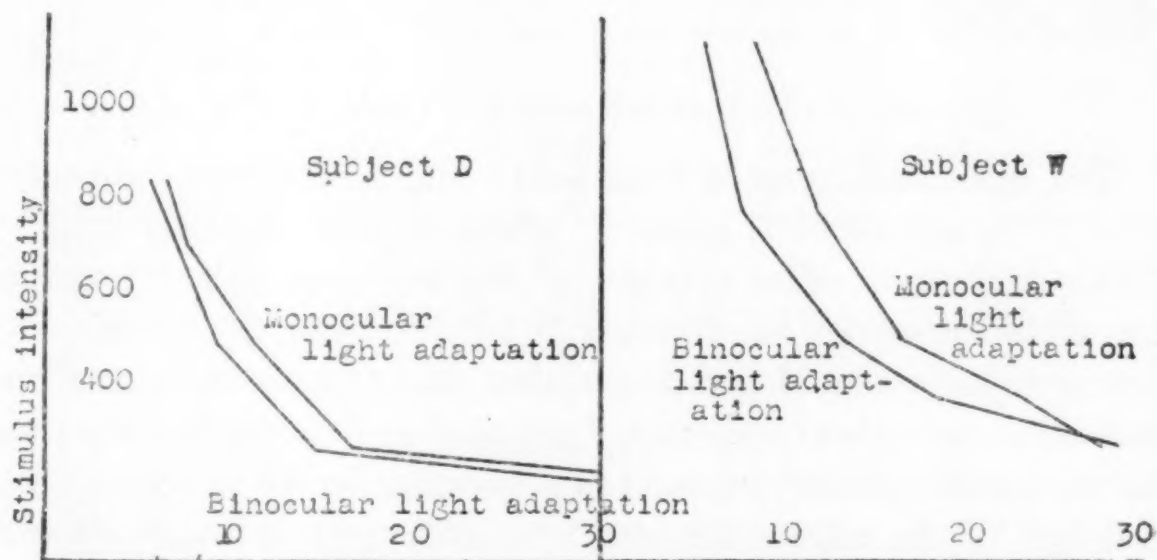
FIG. 4. Effect of Monocular and Binocular Light Adaptation on Thresholds in 30 sec. Dark Adaptation.

mined some time later than the first three variations, and it seemed desirable in view of the possibility of change in objective and subjective conditions to compare monocular and binocular light adaptation data obtained at the same time.

Two subjects, Mrs. Cook (D) and the writer (W) took part in this experiment. They were alternately experimenter and subject. For (1), (2), and (3) above, there were usually 4 or 5 experimental periods each day. The distribution of the periods of experimentation with the right eye, left eye, and binocular vision was arranged to equalize variation with time of day and from day to day. For the comparison of the effect of monocular and binocular light adaptation on later threshold determinations with the left eye, 4 series of observations were made each afternoon, one monocular and one binocular (light adaptation) with each subject. The schedules of stimulus intensities were made up by the writer at the beginning of the experimental work and each experimenter kept the one followed by the other. The order for any given day was unknown to the subject.

The results are given in Tables I and II and Figs. 3 and 4. Stimulus intensities are given throughout in the arbitrary scale of light units described in the photometric section.

The general results support the hypothesis of the existence of binocular " summation " and also show an advantage of binocular over monocular light adaptation. A more detailed discussion is given below.

(1) BINOCULAR SUMMATION (Table I, Fig. 3)

The binocular curve is lower than either monocular throughout. The difference is greatest, however, near the beginning of dark adaptation. The average of the left and right monocular threshold intensities for Subject D 5.8 sec. after the cessation of light adaptation is 73 per cent higher than the binocular. From this point the curves approach gradually so that the last monocular threshold intensity exceeds the binocular by 42 per cent. For Subject W the monocular-binocular difference is more marked. At the earliest time that permits a comparison of all three curves, 9.22 sec., the average monocular is 120 per cent higher than the

binocular, while the left-right average corresponding to the end point of the binocular curve lies 57 per cent above the latter.

(2) Left lower (left eye) thresholds after binocular than after monocular light adaptation. This result, which was the reverse of expectation, must be taken into account in evaluating the summation effects in Fig. 3. There the left and right thresholds were taken after monocular light adaptation. If we bring the left and right eye curves of Subject D in Fig. 3 to the level they would have reached if taken after binocular light adaptation, by correcting the average of Subject D's left and right monocular thresholds (Fig. 3) for the percentage of difference between that subject's thresholds after monocular and binocular light adaptation (Fig. 4), the 73 per cent becomes 50 per cent, and 42 per cent becomes 35 per cent. A like computation for Subject W reduces 120 per cent to 50 per cent and 57 per cent to 30 per cent. The " summation " effects for these subjects are thus in close agreement. Their differences seem to lie in amount of influence of binocular light adaptation on monocular observation.

An attempt was made to carry out a similar experiment with 3 other subjects. The procedure differed slightly. (1) Binocu-

TABLE I

Monocular and binocular thresholds during the first 30 sec. of dark adaptation. Pre-dark adaptation—15 minutes. Light adaptation—1 minute. Dark adaptation—2 minutes. Each time is an average of 10 determinations. Graph in Fig. 3.

	Subject D			
	Left	Right	———Binocular———	
Stimulus intensity	Time in seconds	Time in seconds	Stimulus intensity	Time in seconds
1082	4.76	5.39		
821	5.71	6.50	500	5.80
559	8.59	9.86	300	9.82
292	16.96	18.92	200	17.17
213	24.36	22.90	150	23.78
	Subject W			
1082	7.7	9.22		
840	10.6	10.63	840	5.02
559	13.69	14.96	559	7.71
421	16.46	22.40	421	9.90
292	23.00	25.13	292	16.45
			210	22.10

lar light adaptation was used throughout. (2) Fifteen light adaptation and dark adaptation periods were given in each session. (3) Only 3 stimulus intensities were tested. (4) An equal number of left, right, and binocular thresholds were taken in each session.

Eventually results were obtained from only 1 subject (P). The reasons for change of procedure with the other two (T and C) are discussed later. P's results proved so variable as to be extremely difficult of interpretation. This subject was quite

TABLE II

Left eye thresholds during the first 30 sec. of dark adaptation after monocular and binocular light adaptation. Each time av. of 10 thresholds.
Graph in Fig. 4.

Subject D

	Stimulus intensity	836	700	485	250	181
Monocular light adaptation	Time	6.30	7.25	11.20	21.43	32.60
Binocular light adaptation	in seconds	5.69	6.96	9.11	19.76	29.85

Subject W

	Stimulus intensity	1132	765	485	355	250
Monocular light adaptation	Time	7.95	11.37	16.12	23.08	27.07
Binocular light adaptation	in seconds	5.41	7.52	12.98	18.37	28.01

TABLE III

Subject P. Monocular and binocular thresholds during the first 30 sec. of dark adaptation. Light adaptation—1 minute, dark adaptation—2 minutes. Each value average of 5 thresholds.

Averages of all thresholds

Intensity	Left	Right	Binocular
600	6.90 sec.	15.30 sec.	8.00 sec.
355	11.36 "	23.54 "	13.74 "
250	23.48 "	25.40 "	13.10 "

TABLE IV

Same as Table III with doubtful cases excluded.

Averages with doubtful cases excluded

Intensity	Left	Right	Binocular
600	9.30 sec.	15.40 sec.	6.00 sec.
355		18.90 "	16.06 "
250	31.45 "	28.80 "	15.70 "

dissatisfied throughout and gave many reports of bad fixation or observation. Accordingly the data are not presented graphically, but the averages are given in Tables III and IV. In general the binocular thresholds are lower than either right or left, especially with the doubtful cases excluded. The fewness of the remaining determinations, however, forbids attaching much importance to them.

B. *Monocular and Binocular Thresholds During 10 Minutes Dark Adaptation*

As before there was 15 min. initial dark adaptation followed by 1 min. light adaptation. With one exception either 5 or 6 cycles of successive light adaptation and dark adaptation made up one period of experimentation. The outline of a sample session is as follows:

Adaptation	D	L	D	L	D	L	D	L	D	L	D
Minutes	15	1	10	1	10	1	10	1	10	1	10

Threshold judgments were made during the 10 min. dark adaptation periods at 1 min. (in one series 45 sec.), 4 min., 7 min., and 10 min. after the end of light adaptation.

The work in Part A might be called " intensive " because of the number of threshold judgments taken within a few seconds of each other. In Part B, Part C, and Part D no threshold was taken earlier than 1 min. after the cessation of light adaptation, and all thresholds are 3 or 4 min. apart. Other differences are noted in the earlier description of apparatus and procedure and are further elaborated in the discussion of the curve of foveal dark adaptation in Part D.

Slightly varied procedures make it desirable to deal separately with the experimental data from each of the four subjects.

(1) SUBJECT D

(a) The data shown below were gathered in one day's experimenting.

	45 sec.	4 min.	7 min.	10 min.
Left	192.1	48.4	29.6	26.6
Right	176.0	50.3	28.3	24.0
Binocular	139.3	41.3	24.6	24.1

This day's work consisted of 2 cycles, one of 9 units of successive light adaptation and dark adaptation (10:30 A.M. to 12:40 P.M.), and one of 6 successive light adaptation and dark adaptation units (1:15 P.M. to 3:00 P.M.). Twenty minutes of dark adaptation preceded each period of experimentation. The right, left, and binocular thresholds were distributed to balance fatigue, practice, and time of day. The two experimental periods may be outlined:

Eye		B	B	R	R	L	L	R	R	B	B	L	L	B	B	R	R	L	L
Minutes	20	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10

Intervening half-hour of moderate light adaptation.

Eye		L	L	R	R	B	B	L	L	R	R	B	B
Minutes	20	1	10	1	10	1	10	1	10	1	10	1	10

The resulting data are thus averages of 5 observations after 45 sec., 4 min., 7 min., and 10 min., respectively.

This experiment permitted a satisfactory comparison of the sensitivity of the right eye and left eye, since their thresholds were taken under like conditions and in the same sessions. It seemed improbable, however, that the relation of monocular to binocular thresholds could be accurately estimated with this procedure. As may be seen from the above outline, monocular light adaptation preceded both right and left monocular observation. This resulted in one eye being differently dark adapted from the other before some light adaptation periods. For example, before the second light adaptation in the first session, both eyes had been dark adapting for 10 min. Since only the
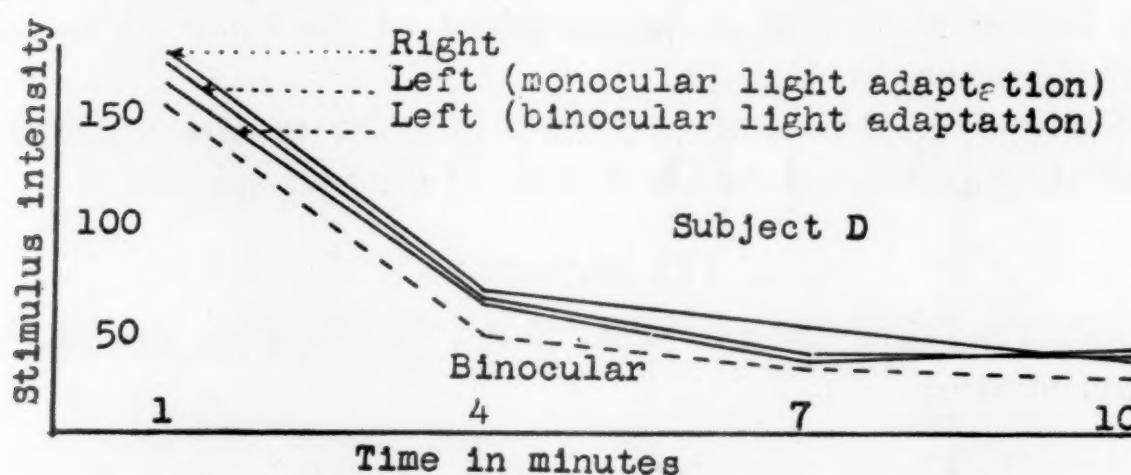
FIG. 5. Thresholds in 10 min. Dark Adaptation.

right eye was then light adapted, the left, before the third light adaptation, had 20 min. of dark adaptation. Similarly, in the fifth cycle the left eye was dark adapted 20 min. before binocular light adaptation, while the right had been dark adapted only 10 min. If, as is possible, the 1 min. light adaptation did not bring the eye to the same level after 20 min. as after 10 min. dark adaptation, such a discrepancy between the two eyes might prevent their complete coöperation in binocular observation and give a higher binocular threshold than the true one.

(b) Accordingly the procedure was changed so that the right, left, and binocular threshold judgments were made in separate sittings. Two periods of experimental work consisting of 5 successive repetitions of light adaptation and dark adaptation were carried through for the right eye with monocular light adaptation, left with monocular and binocular light adaptation, and binocular with binocular light adaptation. The results comprise a total of 10 observations for each of the four points on the four curves. The first observation was made at the end of 1 min., instead of 45 sec. as in (a). The experiment lasted 4 days (Nov. 19 to 23) with 2 periods of experimentation each

TABLE V

Binocular and monocular thresholds during 10 minutes dark adaptation following 1 minute light adaptation. Data plotted in Figs. 5, 6, and 7.

Subject D

Each value an average of 10 thresholds

	1 min.	4 min.	7 min.	10 min.
Right—monoc. lt. ad.	177.0	66.7	50.9	37.9
Left —monoc. lt. ad.	171.5	65.3	39.4	35.4
Left —binoc. lt. ad.	163.0	64.7	37.6	39.6
Binocular	135.6	47.4	33.5	28.0
Av. monocular value when binocular = 100	122	139	129	138

Subject W

Each value an average of 12 thresholds

	1 min.	4 min.	7 min.	10 min.
Right—binoc. lt. ad.	209	110.4	74.2	64.2
Left —monoc. lt. ad.	265	135.6	94.4	82.1
Left —binoc. lt. ad.	237	122.4	97.8	82.8
Binocular	164	86.4	48.6	44.0
Av. monocular value when binocular = 100	136	135	177	167

day. Right and binocular thresholds were taken on the first and
last days, the left-monocular and left-binocular on the two inter-
vening days. Comparison of the right with the binocular, and
the left-monocular with the left-binocular is thus free from day
to day variation. The averages of the 10 thresholds taken at
each point are shown in Table V and plotted in Fig. 5.

The data for a 10 min. dark adaptation period following 1 min.
of light adaptation thus agree with the results previously
reported for the same subjects during the first 30 sec. of dark
adaptation. The binocular thresholds are lower than either
monocular, the left eye is more sensitive than the right, and
binocular light adaptation followed by left eye observation gives
lower thresholds than monocular light adaptation. The bottom
row (Subject D) in Table V gives the binocular-monocular rela-
tion in percentages. To get these percentages the right eye
thresholds were first corrected for the percentage of difference
between the monocular and binocular light adaptation results for
the left eye. The corrected thresholds for the right eye were
then averaged with the left eye thresholds for binocular light
adaptation and this average expressed as a percentage of the
binocular.

(2) SUBJECT W

The left, right, and binocular comparison for Subject W
(Fig. 6) was similar to (a) of Subject D, except that binocular
light adaptation was used for all three kinds of observation, and
that 6 (2 left, 2 right, 2 binocular threshold observation) repe-
titions of 1 min. light adaptation and 10 min. dark adaptation
were made in each sitting. Left, right, and binocular thresholds
were distributed to equalize fatigue and practice.

As in Part A, Mrs. Cook (D) acted as experimenter while
the writer (W) was subject. It should be noted that when acting
as subject, the precaution I used with other subjects of keeping
them in ignorance of the trend of their results could not be
observed. In posting and computing each day's results I neces-
sarily became acquainted with my own. The possibility of an
" error of expectation " thus existed. In Part (A) such a

possibility was avoided by having the five stimulus intensities arranged in semi-random order. In Part (B) an adjustable slide behind the light adaptation screens served the same purpose. The slide could be set to cover the right or left eye, or removed to allow binocular observation. The " setting " was done by the experimenter during light adaptation. The device proved so effective that I could detect no difference between trials. At all times I seemed to be using both eyes. To avoid inference from the schedule arrangement the six daily lists were given to (D) before the beginning of the experiment and used in chance order.

The thresholds measured after monocular light adaptation of the left eye were taken in 2 periods, one on the first and one on the last day of the experiment. One period came in the early part, the other in the later part of the day's work. Table V and Fig. 7 give W's results. In presence and amount of binocular summation, the latter are similar to the results of Subject D in Fig. 5. The curves in Figs. 5 and 7 differ in regard to the relative sensitivity of the right and the left eye, D's left and W's right eye being the more sensitive. In this respect W's results differ also from the results of the same subject for the first 30 sec. of dark adaptation. (Fig. 1.) Possible explanations of the change in the relative sensitivity of W's eyes are: (1) A real difference in the relative sensitivity of the two eyes in the first
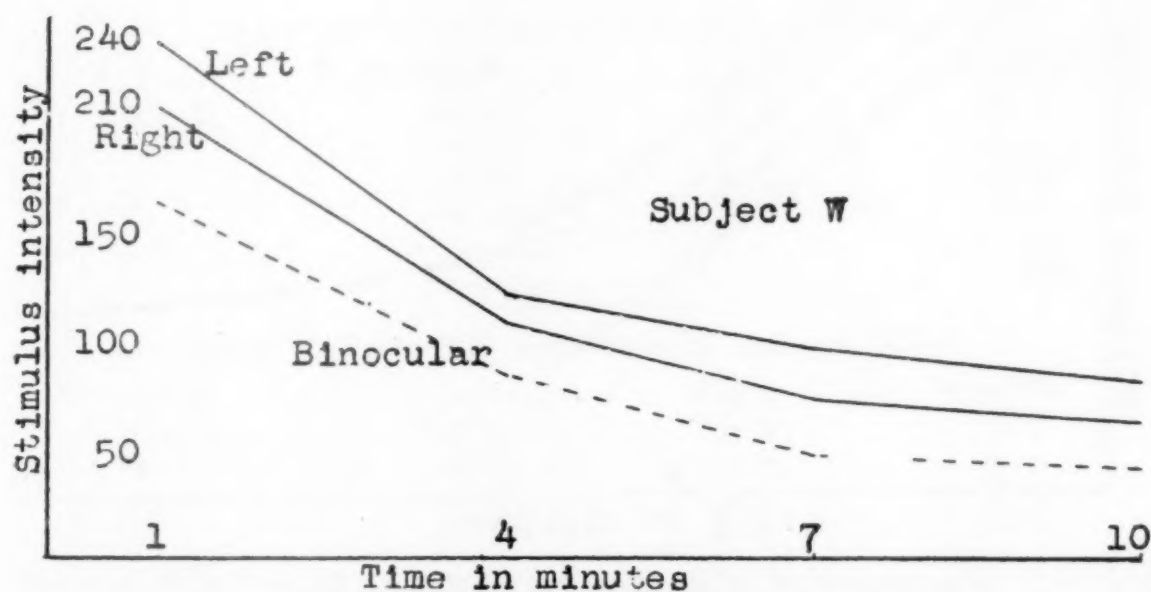
FIG. 6. Thresholds in 10 min. Dark Adaptation.

30 sec. and in later dark adaptation. (2) Some change in the apparatus during the interval between the two experiments. The results of other subjects make this explanation highly improbable. (3) Variation in the relative sensitivity of the two eyes from one experiment to the next. The important point, however, is that the binocular thresholds are again lower than those for either eye. The amount of monocular-binocular difference is expressed in percentages in Table V, Subject W. The first two average monocular values exceed the binocular by 35 per cent, which is close to the amount of summation with Subject D and also for the last set of determinations of W's thresholds during the initial 30 sec. of dark adaptation. After 7 and 10 min. of dark adaptation W's monocular thresholds exceed the binocular by about 70 per cent.

The after-effect of binocular light adaptation on monocular observation is the same for both subjects. Comparing their results from the beginning of dark adaptation to the end of 10 min., we see that: (1) Binocular light adaptation gives lower thresholds than monocular light adaptation, for both subjects. (2) The effect is greatest at the beginning of dark adaptation, and has vanished four minutes after the cessation of light adap-
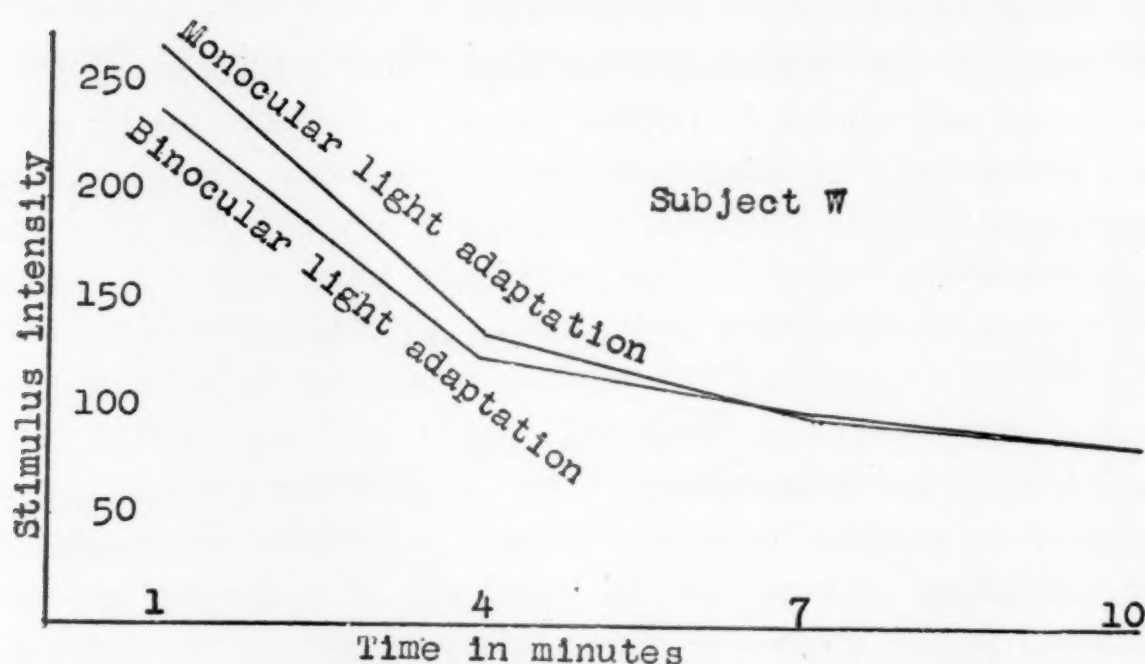
FIG. 7. Comparison of Monocular and Binocular Light Adaptation on Left Eye Thresholds in 10 min. Dark Adaptation.

tation with Subject D and two minutes later with Subject W.
(3) The amount and duration of the after-effect are greater for
W than D.

(3) SUBJECT P

With Subject P and Subject C binocular summation alone was
investigated. Light adaptation was binocular throughout. Pro-
cedure deviated only slightly from that with Subjects D and W.
Each period of experimentation was divided into 15 min. pre-
liminary dark adaptation, and 5 repetitions of 1 min. light
adaptation followed by 10 min. dark adaptation. Thresholds
were taken during dark adaptation 1, 4, 7, and 10 min. after
light adaptation had ended. The experiment comprised 4 periods
of experimental work, so each average in Tables VI, VII, and
VIII represents 5 to 7 thresholds. Threshold observations were
divided between left, right, and binocular in such a way that, as

TABLE VI
Averages of gross thresholds.
Subject P

Time	Left	Right	Binocular
1 min.	238.0	172.0	144.0
4 "	75.5	44.6	45.0
7 "	61.1	37.2	43.0
10 "	44.6	32.3	37.2

TABLE VII
Averages of averages of each day's thresholds.

Time	Left	Right	Binocular
1 min.	238.0	168.0	153.0
4 "	66.5	44.7	42.5
7 "	56.0	36.7	40.8
10 "	42.7	34.8	35.0

TABLE VIII
Same as Table VII with doubtful cases excluded.

Time	Left	Right	Binocular
1 min.	238.0	168.0	153.0
4 "	66.5	51.0	44.9
7 "	44.8	32.7	25.6
10 "	41.6	34.8	36.6

Tables VI, VII, VIII. Subject P. Binocular and monocular thresholds
during 10 min. dark adaptation following 1 min. binocular light adaptation.

nearly as possible, an equal number of the three fell in each sitting.

The data show great variability, both from day to day and within a given period. Subject P also found difficulty in deciding, and gave many reports of loss of fixation, presence of glare, and other subjective light phenomena. It was thus thought best to treat the data in three ways. Table VI gives averages of gross thresholds; Table VII averages of each day's averages. The latter method of treating the results was intended to correct the unequal number of right, left, and binocular thresholds sometimes taken in any one day. Table VIII gives the averages after dropping all for which the subject reported bad fixation or was otherwise doubtful. In general the binocular is lower than either monocular, though the gross data show a fair correspondence between the binocular and right thresholds. This, combined with the variability and scantiness of the data forbids any final conclusions being drawn.

(4) SUBJECT C

The original plan with Subjects P and C included experimental work on the first 30 sec. of dark adaptation (Part A), and a later experiment covering the period from 1 to 10 min. after the cessation of light adaptation (Part B). For Subject P this project was completed, but the variability of Subject P in the work reported in Part A (first 30 sec. of dark adaptation) made it unlikely that a similar experiment with Subject C would give reliable data without a great deal of practice. Accordingly no threshold judgments were made by C during the first 30 sec. of dark adaptation. Threshold determinations were first made with C after 1 min. dark adaptation. Otherwise the procedure was the same as for Subject P in Part B. The resultant averages of 5 individual thresholds for each value are:

	1 min.	4 min.	7 min.	10 min.
Left	133.2	58.8	34.0	31.1
Right	106.0	58.2	27.5	37.8
Binocular	90.2	28.0	16.5	13.7

There results correspond to those of D and W. The fact that three subjects reported (later) in Part C showed results of a

different kind, however, made it desirable to take more threshold observations with Subject P. The latter was therefore asked to make 3 additional sets of threshold judgments, with the same procedure as before, except that there were 6 series of 1 min. light adaptation and 10 min. dark adaptation in each experimental period:

Observing eye.

Feb.	7, 1929	B	R	L	L	R	B
Feb.	11, 1929	R	L	B	B	L	R
Feb.	13, 1929	L	B	R	R	B	L

Binocular light adaptation was used throughout. The averages of the six thresholds are:

	1 min.	4 min.	7 min.	10 min.
Left	156.1	50.1	27.4	23.6
Right	169.3	74.1	31.4	20.4
Binocular	128.0	49.2	19.5	16.2

Again the binocular are lower, and the amount of difference is close to that of D and W. The combined averages of these two experiments (11 thresholds) appear in Fig. 8. In percentage terms, the average monocular is higher than the binocular at the 1, 4, 7, and 10 min. points by 32, 50, 66, and 80 per cent respectively. The mean of the four is 57 per cent. Subject C was satisfied with the accuracy of judgment and reported few doubtful cases. The only difficulty, reported by all subjects, was that of
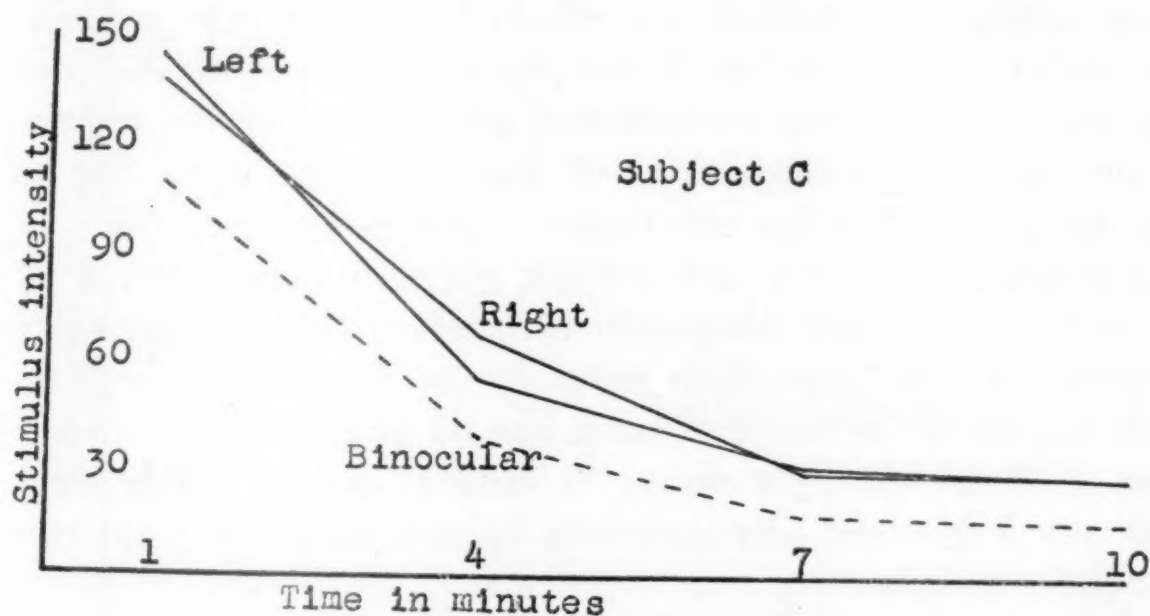
Fig. 8. Monocular and Binocular Thresholds during 10 min. Dark Adaptation.

deciding on a criterion of " thereness " of the stimulus. There was almost always a brief period between the beginning of awareness of " something there " and the " clearing up " of the circular disc of light. All subjects felt that the degree of clearness of the impression varied somewhat from time to time.

C. *Monocular and Binocular Thresholds During 15 Minutes Dark Adaptation*

The procedure in Part C differs from that of Parts A and B: (1) The length of the light adaptation was 3 min. instead of 1 min. (2) The length of the period of threshold taking in dark adaptation was 15 min. instead of 10 min. (3) In Part C, thresholds were taken a few seconds after the beginning of dark adaptation, as well as at the 3, 7, 11, and 15 min. points. The preliminary dark adaptation lasted 20 min. In all cases this was followed by 3 successive repetitions of 3 min. light adaptation and 15 min. dark adaptation. The 5 subjects who took part in the experiment fall into two groups.

GROUP I

With Group I (2 subjects) light adaptation was always binocular. One left, 1 right, and 1 binocular series of threshold observations were made in each experimental period, the order being arranged to balance the effects of fatigue and practice. The slide mentioned in Part B was placed in front of the stimulus and set for right, left, or binocular observation by the experimenter during light adaptation. It seemed to the subject that he was using both eyes for observation. There were 6 periods of experimental work with each subject, giving 6 values after 3, 7, 11, and 15 min. dark adaptation with left, right, and binocular observation. For thresholds taken in the first few seconds of dark adaptation the stimulus lamp was set at either of two positions (700 or 485 light units) in random order. There were thus only 3 threshold determinations by each subject at these two stimulus intensities.

The data obtained appear in Table IX and Figs. 9 and 10. The two values for the first threshold taken are not shown graphi-

cally because the rapid drop in the first few seconds of dark adaptation with the succeeding relatively slow descent bring the curves so close to the left and base lines, when these two separate trends
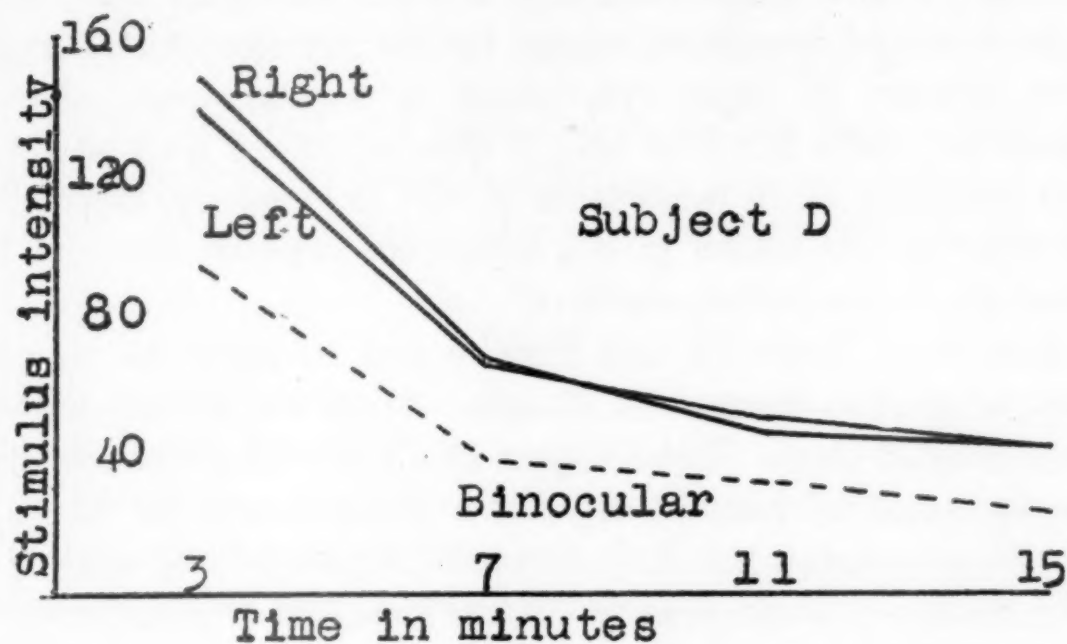
FIG. 9. Thresholds in 15 min. Dark Adaptation.
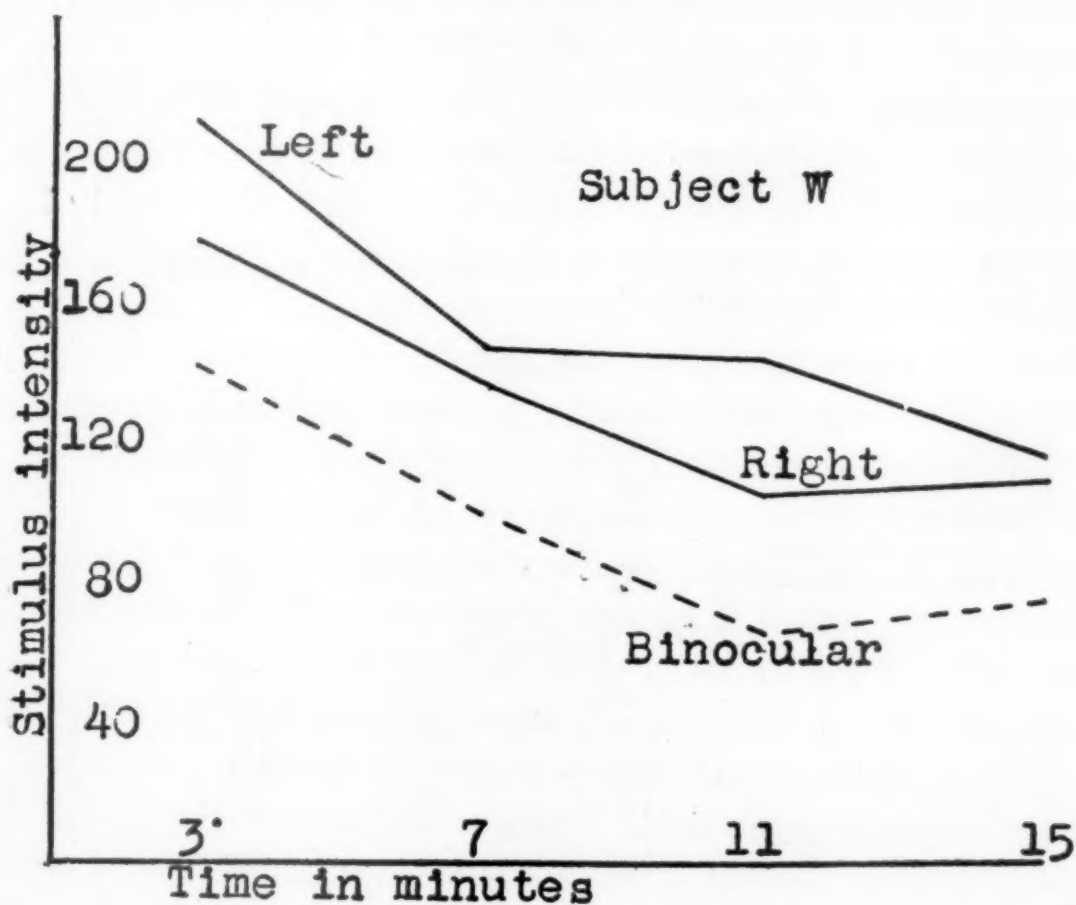
FIG. 10. Thresholds in 15 min. Dark Adaptation.

are plotted on a small sheet of paper, that the real differences
between the curves are obscured.

Part A of the above table, which gives data from the first few
seconds of dark adaptation, shows lower binocular than left or
right threshold intensities, except for the average initial threshold
with Subject D, right eye, which is slightly lower than the
binocular. The fact that only 3 determinations were made for-
bids attaching much importance to this discrepancy, especially as
all other results which give a difference between left and right
show the former more sensitive.

Part B of Table IX and Figs. 9 and 10 show the course of
dark adaptation from 3 to 15 min. Here the greater binocular
sensitivity is clear. For Subject D (Table IX) the average of
the right and left thresholds exceeds the binocular by 52, 70, 48,
and 65 per cent at the 3, 7, 11, and 15 min. points, respectively.
The mean of these four is 59 per cent. For comparison the

TABLE IX

Binocular and monocular thresholds during 15 min. dark adaptation following
3 min. light adaptation.

Intensity	⎯⎯Subject D⎯⎯		⎯⎯Subject W⎯⎯	
	700	485	700	485
Right	10.3 sec.	22.2 sec.	19.1 sec.	21.8 sec.
Left	14.1 "	21.1 "	15.3 "	22.2 "
Binocular	10.8 "	14.3 "	14.1 "	18.9 "

A. First thresholds in number of seconds before appearance of stimulus.
Each point av. of three thresholds.

Subject D

	3 min.	7 min.	11 min.	15 min.
Right	147.2	67.4	46.7	41
Left	139	65.8	50.7	40.2
Binocular	94	39	32.9	24.5
Av. monocular value when binocular =100	152	170	148	165

Subject W

	3 min.	7 min.	11 min.	15 min.
Right	177	134.3	105.6	110
Left	211.6	147.4	144	116
Binocular	141.2	99.3	65.7	76.7
Av. monocular value when binocular =100	138	142	190	147

B. Thresholds after 3 to 15 minutes dark adaptation. Each value average
of 6 thresholds.

corresponding percentages for W in Part C; for D and W in Part A; and for D, C, and W in Part B are given.

Subject	Part A		Part B	Part C
D	50	35	32	59
C			57	
W	50	30	54	54

The average left and right thresholds are thus about 50 per cent higher than the binocular; halfway between complete " summation " and absolute lack of coöperation between the two eyes.

GROUP II

The second group consists of 3 subjects (H, N, and S). Although reported last, the experimental work with Group II was begun first. On account of the expected inhibitory influence of light adaptation of the non-observing eye on monocular thresholds, only the eye which later observed the threshold stimulus was light adapted. This made it seem desirable to take only one kind of threshold (left, right, or binocular) in any one experimental period. It was found, however, that it was more important to control the day to day variability, so in the later part of the experiment left, right, and binocular threshold judgments were made in the same sitting. Only one of these three types of observation was used in any one 15 min. of dark adaptation. Three minutes of light adaptation intervened between each shift from right to left, left to right, or monocular to binocular threshold observation. Eight sittings were given to each subject. On account of the difference in results * between Group II and the other subjects, the project of testing the effect of monocular and binocular light adaptation on monocular thresholds was abandoned for N and H, and the available time spent on summation. The method of taking the initial threshold in the first seconds of dark adaptation was at first the same as for Group I. The results of this initial experimental work are given in Tables X, XI, and XII. These proved so variable and inconsistent that it was decided to discontinue the attempt. Accordingly, with N and S the first judgments were made after 1 minute dark adaptation.

* Discussion below.

Inspection of the data (now to be given) shows that binocular thresholds for the 3 subjects in Group II are slightly lower than the thresholds of the more sensitive eye. In evaluating this " summation," however, it should be noted that monocular light adaptation preceded the monocular thresholds, while binocular light adaptation of course preceded binocular threshold observation. But for Subjects D, S, and W (Figs. 4, 5, 7, 11) monocu-

TABLE X

Initial thresholds of 15 min. dark adaptation period.

Subject H

Right			Binocular	
Seconds	Intensity		Seconds	Intensity
3.4	802		13.0	816
38.0	802		13.3	816
20.3	802		17.7	802
25.6	802		3.4	802
16.8	678		9.6	802
12.3	678		19.0	489
4.0	292			
105.0	193			

TABLE XI.

Initial thresholds of 15 min. dark adaptation period.

Subject N

Right			Binocular	
Seconds	Intensity		Seconds	Intensity
6.6	595		11.4	500
4.0	500		2.5	500
8.0	500		18.2	500
39.5	500		3.0	678
23.5	500		at once, bright	625
14.4	500		over a minute	342
13.4	500			
3.5	500			

TABLE XII

Initial thresholds of 15 min. dark adaptation period.
Subject S

Right			Binocular	
Seconds	Intensity		Seconds	Intensity
3	625		3	625
25	500		24	595
25	312		20	500
53	230		4	312
			64	221
			33	400
			60	198
			31	193

lar thresholds are lower after binocular than after monocular light adaptation. It therefore seems probable that if monocular and binocular thresholds for Subjects N and H had both been preceded by binocular light adaptation, there would have been no significant differences between the monocular and binocular thresholds. The observers would thus fall into two classes, one (C, D, W) whose left and right eyes coöperate in binocular observation to give greater sensitivity, and a second (H, N, S) with whom the binocular thresholds approximate those of the more sensitive eye. It seems advisable, however, to consider the data obtained from each of the three subjects in more detail.

(1) subject h

The data from Subject H were obtained in two investigations.

(a) A right-binocular comparison made in 4 working periods from October 20 to November 16, at 10:30 A.M. Two of these sessions were binocular, 1 right, and 1 both right and binocular, making 6 binocular and 4 right eye thresholds for each value.

	3 min.	7 min.	11 min.	15 min.
Right	121.0	59.6	42.3	38.3
Binocular	71.4	37.1	35.2	30.6

Here the binocular thresholds are much lower than the thresholds for the right eye.

(b) A left-binocular comparison in 4 experimental periods from January 10 to 31, 1929. Binocular and monocular thresholds were determined in all periods. The left values are averages of 6 and the binocular of 4 thresholds.

	3 min.	7 min.	11 min.	15 min.
Left	68.5	35.6	23.5	21.3
Binocular	53.8	29.6	22.6	19.0

In comparing left eye and binocular thresholds with Subject H for the first few seconds of dark adaptation, the procedure was changed slightly to allow the subject a few seconds after light adaptation for adjustment before the stimulus appeared. When he signaled (reaction key) that he was ready, the stimulus switch was closed and the lamp moved up as in later thresholds. The method proved quite successful, as is shown by the slight vari-

ability of H's first thresholds as compared with the values in Tables X, XI, and XII.

(2) SUBJECT S

The experimental work with Subject S consisted of: (a) 2 sessions, 1 with right eye threshold judgments on October 17, and 1 with binocular threshold observation on October 19, and (b) 6 sessions in which binocular thresholds, right eye thresholds with monocular light adaptation, and left eye thresholds with both monocular and binocular light adaptation, were taken in each session. Experimental work always began at 5 P.M. The data show the right eye more sensitive than the left, and the right and binocular close together. Averages of 4 to 6 thresholds are given.
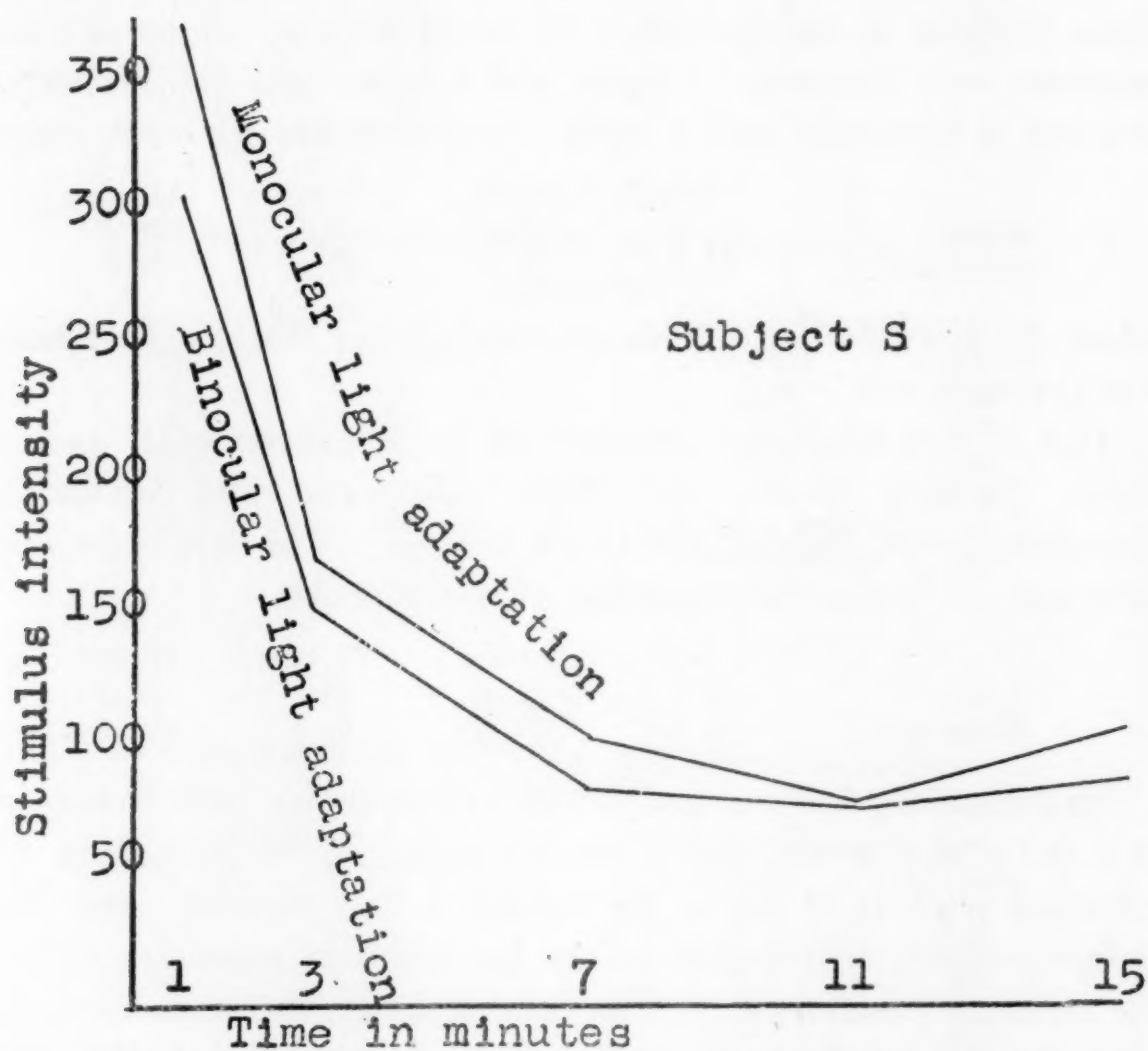

FIG. 11. Comparison of Effect of Monocular and Binocular Light Adaptation on Thresholds in 15 min. Dark Adaptation. Left Eye.

	1 min.	3 min.	7 min.	11 min.	15 min.
Right (monoc. lt. ad.)	338.0	151.3	68.8	56.1	55.6
Left (monoc. lt. ad.)	367.0	167.0	100.0	74.3	102.5
Left (binoc. lt. ad.)	304.5	150.0	81.5	73.1	85.0
Binocular	245.0	159.0	71.8	49.3	45.0

The lower right eye thresholds at the 3 and 7 min. points are due to the fact that the thresholds for that eye on October 17 were slightly lower than the binocular limens taken 2 days later. A more accurate right-binocular comparison can be obtained from the data of two experimental sessions on successive days, in which right and binocular thresholds were determined in both sessions, thus equalizing the day to day variability for right and binocular observation. Averages of 3 thresholds are given.

	1 min.	3 min.	7 min.	11 min.	15 min.
Right	379.0	190.3	67.7	54.3	28.2
Binocular	269.5	170.3	70.0	52.7	28.2

The experiment yielding the data in Fig. 11, which represents thresholds of the left eye after binocular and monocular light adaptation, was among the best controlled of all our investigation. Threshold observations were made after both binocular and monocular light adaptation, in each period of experimentation, thus eliminating day to day variability. Since this part of the work came near the end of the experiment the subject had at least 10 full sessions of practice. The resulting lower thresholds after binocular as contrasted with monocular light adaptation support the results of Subjects D and W on the same problem. (Figs. 4, 5, 7.) The effect seems to last 10 min. for Subject S, 4 min. for Subject D, and 6 min. for Subject W. The difference between the results for S on the one hand and D and W on the other, may be due to the length of the light adaptation period, which was 3 min. with S and 1 min. with D and W.

(3) SUBJECT N

The results of the threshold determinations for Subject N appear in Table XIII. Except for thresholds after 1 min. dark adaptation, the values in Table XIII are averages of 6 thresholds for the left eye and 9 thresholds each with right and binocular observation. The 1 min. values are averages of 4 thresholds.

The whole experiment comprised 8 working periods of 3 successive light and dark adaptation cycles each.

The data in Table XIII show a slightly lower right than left, and binocular than right. It is probable, however, that the right-

TABLE XIII

Binocular and monocular thresholds during 15 min. dark adaptation following 3 min. light adaptation.

Subject N

	1 min.	3 min.	7 min.	11 min.	15 min.
Left	384.0	120.9	52.1	42.6	38.1
Right	335.0	112.2	48.1	41.3	33.7
Binocular	340.0	103.1	47.5	35.7	34.5

binocular difference may be accounted for by the monocular light adaptation of the right eye. More data were desired for this subject, particularly on the effect of monocular and binocular light adaptation on later monocular thresholds, but lack of time prevented.

D. *The Foveal Dark Adaptation Curve*

(1) Investigation of 2 types of foveal dark adaptation. Thresholds taken during 1 hour continuous dark adaptation.

As mentioned in Part B, it was originally intended to carry out an experiment with Subject T similar to the work done with Subjects C and P and reported in Part B. After 2 sessions (5 successive repetitions of 1 min. light adaptation and 10 min.

TABLE XIV

Binocular and monocular thresholds during 10 min. dark adaptation following 1 min. binocular light adaptation.

Subject T

	1 min.	4 min.	7 min.	10 min.	
Binocular	128.0	74.0	30.6	19.7	
Left	125.0	18.2	31.1	25.6	December 5,
Right				27.4	1928, 1:00 P.M.
Binocular		22.7	12.0	9.6	
Right	114.0	21.3	12.3	12.7	
Left	118.0	22.6	16.2	10.5	
Binocular	53.0	12.7	6.5	5.1	
Right	85.0	11.8	8.5	4.7	December 5,
Left	28.5	11.0	8.9	6.3	1928, 1:00 P.M.
Right	73.0	19.8	8.8	6.3	
Binocular	16.0	6.2	6.7	4.5	

dark adaptation), however, it became evident that some change should be made, either in the length of the time of light or dark adaptation, or in both. The individual thresholds appear in Table XIV.

On first inspection two things stand out: (a) Wide variability from one series to another. (b) Low thresholds compared with other subjects. A second glance shows a regularity in the irregularity. Within any one series (after each light adaptation) there are strikingly few reversals. Also the variability is to a great extent progressive. Thresholds are lower after each successive dark adaptation and light adaptation. It seemed probable, therefore, that the subject was not brought back to the some condition by each successive light adaptation. Accordingly the procedure was changed. The subject was dark adapted 20 min. followed by 3 min. light adaptation, after which thresholds were taken for an hour without further light adaptation. Four such series were taken for the right eye with monocular light adaptation. Only 3 thresholds were secured in the first few seconds: 4 sec., 92.6; 11.3 sec., 95.4; 10.3 sec., 66.3. For comparison purposes one series each with subjects D and W were carried out under similar conditions (20 min. preliminary dark adaptation, 3 min. light adaptation, 1 hour dark adaptation). The only change in procedure was that with Subjects D and W light adaptation was binocular and threshold judgments were made with the right and left eye alternately. The results, together with an additional series of thresholds taken with Professor A. Anderson (A) as subject, appear in full in Table XV. Inspection shows that after the initial rapid drop characteristic of all curves of foveal dark adaptation, the curves of W and the other three diverge. For W dark adaptation is ended in 20 to 25 min., while D and A continue to adapt for 50 min. and T for an hour.

Though the data are not enough to warrant a definite conclusion, certain other facts support the hypothesis that the 4 subjects represent two classes of observers, one with relatively short foveal adaptation and the other with a period of foveal adaptation resembling that of the extrafoveal retina. Such other facts are:

(a) Abney and Watson's discovery (1) of two types of observers, the differences between which fit in readily with the differences between the observers in the present experiment.

(b) The slight difficulty experienced by D, A, and T in holding fixation. Such a result would be expected, since with these 3 subjects the preponderance of parafoveal over foveal sensitivity so characteristic of most subjects after 6 or 7 min. dark adaptation would be minimal or absent.

(c) Neither A nor T could notice any predominance of parafoveal over foveal sensitivity at the end of 50 or 60 min. dark adaptation. To test this the stimulus was adjusted to the foveal threshold (after 50 or 60 min. dark adaptation) and the subject instructed to look away from and back to the stimulus and report any difference in brightness. Then the stimulus was set definitely below the foveal threshold. The subject looked back and forth as before and observed whether the stimulus appeared with extrafoveal stimulation and disappeared when looked at directly. For the writer this procedure gives unmistakable predominance of extrafoveal over foveal sensitivity, beginning a few moments after the cessation of light adaptation and becoming more marked as dark adaptation proceeds. Subject C, tested after 15 min. in darkness, and several other subjects who observed after a longer period of dark adaptation, also reported greater extrafoveal sensitivity. On the contrary, Subjects A and T (after

TABLE XV

Monocular thresholds during one hour dark adaptation. Time in minutes.

Subject A Right eye		Subject T Right eye		Subject D				Subject W			
				Left eye		Right eye		Left eye		Right eye	
Time	Intensity	Time	Intensity	Time	Intensity	Time	Intensity	Time	Intensity	Time	Intensity
0.1	131.0	2.3	34.5	1	114.0	2	195.0	10	71.0	8	127.0
8.3	5.1	2.7	16.5	3	156.4	4	86.0	14	65.5	12	74.0
12.3	6.5	4.3	13.0	6	74.0	8	31.0	18	42.0	16	63.0
15.4	3.9	9.3	8.4	10	51.0	12	31.4	22	29.0	20	38.9
19.5	3.2	12	7.5	14	28.2	16	24.1	26	53.0	24	23.1
23.5	3.2	16	5.2	18	19.2	20	13.2	30	46.0	28	48.0
27.5	2.2	20	4.1	22	13.6	24	17.5	34	42.0	32	28.2
29.6	2.2	24	3.6	26	16.2	28	14.3	38	45.0	36	38.0
32.8	2.2	28	2.8	30	8.8	32	10.6	42	61.5	40	44.0
38.7	2.0	32	3.5	34	9.8	36	10.5	46	53.0	44	33.6
42.2	0.7	36	3.9	38	10.6	40	8.9	50	60.3	48	41.1
46.4	0.8	40	3.2	42	10.3	44	7.8	54	67.0	52	22.0
50.5	0.4	44	3.4	46	8.8	48	7.6	58	56.5	56	33.1
		48	3.1	50	6.9	52	10.1			60	33.3
		52	3.3	54	20.5	56	8.9				
		56	2.5	58	12.3	60	11.9				
		60	2.6	62	11.7	64	8.2				
				66	8.1	68	8.9				

50 to 60 min. dark adaptation) could not see a foveal sub-threshold stimulus with the parafoveal regions of the retina, nor did a foveal supra-threshold stimulus appear brighter when looked at extrafoveally. A few observations by Subject D showed results similar to A and T.

The hypothesis of a difference in the nature of foveal dark adaptation in Subjects A, D, and T on the one hand, and Subject W on the other, is further supported by a study of the course of dark adaptation in D and W from the cessation of light adaptation to the end of an hour. For the first 30 sec. (Figs. 3 and 4) D's thresholds are about two-thirds of W's. During the 10 min. period reported in Part B, the ratio of D's to W's thresholds drops from two-thirds at the beginning to one-half at the end. Here the right eye limens, since they were taken after binocular light adaptation with one subject and monocular light adaptation with the other, must be left out of consideration. The 3 min. light adaptation and 15 min. dark adaptation shows still greater divergence. D's thresholds, expressed as a fraction of W's, are: 3 min., two-thirds; 11 min., a little less than one-half; 15 min., one-third. The experiment reported in Part D indicates further that after 15 min. of dark adaptation W's threshold sensitivity has reached a maximum, while D's thresholds after 50 min. have fallen to one-fourth of their 15 min. value.

It is not possible to determine from the data at hand the proportion of our observers that belongs in each class. The fact that no previous investigators reported foveal dark adaptation for longer than 25 min. indicates that W represents much the larger group. Abney and Watson (1) alone report 3 subjects whose foveal and parafoveal sensitivity was about equal after 30 min. dark adaptation. If a relatively brief period of 15 min. to 25 min. foveal dark adaptation is the rule, and a further increase for an hour or more, the exception, it is not surprising that the relatively few subjects used in previous investigations fell within the larger group. Hecht (23) alone had a sufficient number of subjects to bring out individual differences. The reason for his failure to find any subjects whose foveal dark adaptation resembled the typical course of extrafoveal dark adap-

tation probably lies in his use of an extreme red stimulus. Kohlrausch's results (29) show that adaptation to extreme red is finished in 15 or 20 min. not only at the fovea, but for points 5 and 10 degrees from the retinal center.

(2) Comparison of the effect of 1 min. and 3 min. light adaptation on subsequent thresholds.

Analysis of the effect of 1 min. and 3 min. light adaptation can be made for Subjects D and W by comparing their results as given in Part A and Part B with the data from the same subjects in Part C. The former concerns a 2 min. (A) or 10 min. (B) dark adaptation period preceded by 1 min. light adaptation, the latter 15 min. dark adaptation after light adaptation of 3 min. The results indicate in general lower thresholds after 1 min. than after 3 min. light adaptation. For the first 30 sec. the data in Tables I and II should be compared with those in Table IX, A. Even the comparatively few thresholds taken within 30 sec. after 3 min. light adaptation are sufficient to bring out the differential effect of longer as compared with shorter light adaptation. For example, with subject W, the average time of all thresholds after 3 min. light adaptation for an intensity of 700 light units is 16.2 sec. After 1 min. light adaptation, on
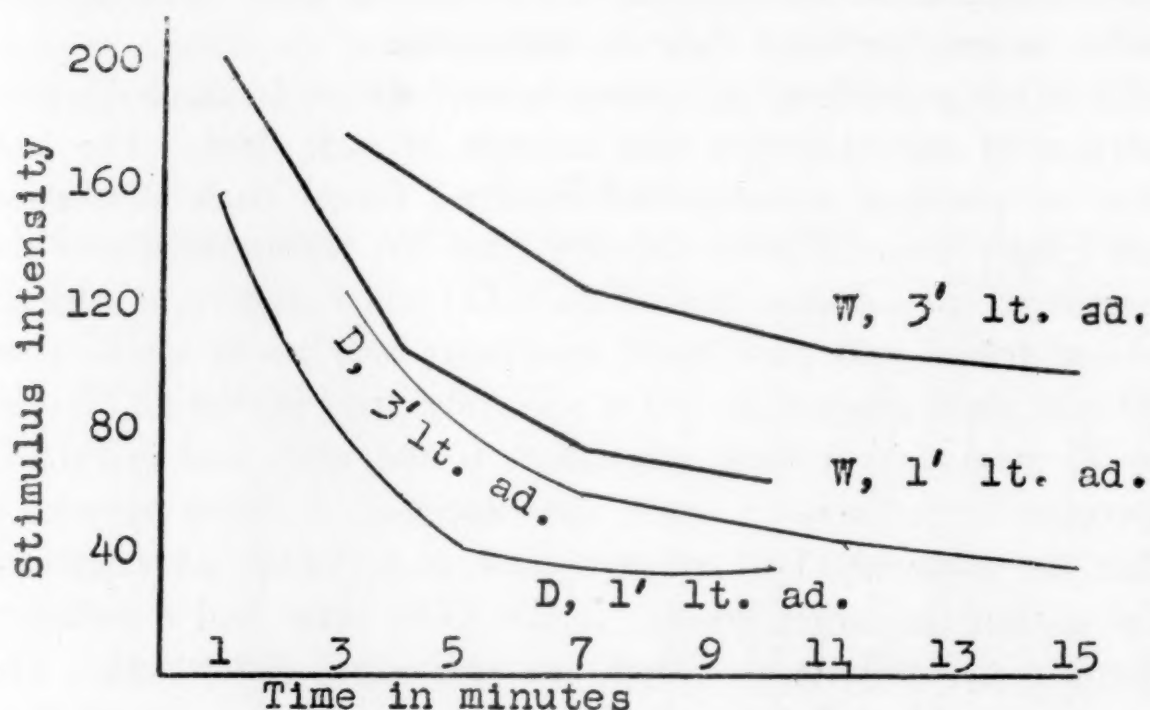

FIG. 12. Effect of 1 and 3 min. Light Adaptation on Thresholds in Succeeding Dark Adaptation.

the other hand, an intensity of 765 is visible to the left eye in 7.5 sec., and an intensity of 559 is at the binocular threshold after 7.7 sec.

The comparison between Part B and Part C is shown graphically in Fig. 12. The points representing W's thresholds are joined by straight lines, and those by D by curved lines. The upper curve for each subject is plotted from thresholds obtained during 15 min. dark adaptation following 3 min. light adaptation, the lower curve for each subject from data gathered in 10 min. dark adaptation after 1 min. light adaptation. Left, right, and binocular values are combined by averaging. The " 3 minute " curves are thus averages of 18 thresholds (Part C), while the " 1 minute " points represent 30 individual thresholds for D and 36 for W. All except the thresholds for the right eye, Subject D, 1 min. light adaptation, were taken after binocular light adaptation. The divergence of D's 1 min. and 3 min. curves before 4 min. dark adaptation is therefore slightly more than appears from the figure. Even without this correction the greater effect produced by 3 min. light adaptation is striking.

(3) Effect of successive periods of light and dark adaptation.*

It will be remembered that each experimental session in Part A consisted of 10 successive repetitions of 1 min. light adaptation and 2 min. dark adaptation. The possibility arose that the light and dark adaptation would not exactly balance each other. Thresholds might be higher or lower after each successive light adaptation. The results are analyzed to uncover possible cumulative tendencies. This is done by multiplying the 5 thresholds for any one serial position * by factors that will bring the 5 to a common level, and averaging the results.

The need for this " leveling " arose from the fact that each of the 5 thresholds for any one serial position was taken with the stimulus at a different intensity. The corresponding threshold numbers (in seconds) are therefore much larger for the low stimulus intensities, and the latter would thus be heavily weighted if the gross thresholds were averaged. An example will make

* See Part A.

this clear. For the first serial position with Subject D, right eye, there were 5 thresholds taken in the first 30 sec. of dark adaptation, one at each of the 5 stimulus intensities given below:

Intensity	1082	821	559	292	231
Seconds	5.1	7.9	9.2	16.5	20.5

These were multiplied by suitable factors and averaged:

$$5.1 \times 10 = 51.0$$
$$7.9 \times 9 = 71.1$$
$$9.2 \times 6 = 55.2$$
$$16.5 \times 3 = 49.2$$
$$20.5 \times 2 = 41.0$$

Ave.   53.6

All thresholds were averaged except those for D with binocular observation. The latter were omitted because there were only 4 points on the curve and only 8 values for the first point (Fig. 3. For explanation see Part A). The averages are given in Table XVI.

The results are most curious and unexpected. Directly opposite trends appear in the results for the two subjects. Successive thresholds are lower for W and higher for D. Moreover, the opposing trends are about equal in amount, so that if the data for the two subjects are combined both tendencies disappear. No adequate explanation of the phenomena occurs to the writer.

TABLE XVI

Analysis of influence of serial position with successive 1 min. light adaptation, 2 min. dark adaptation periods. Each value average of 5 weighted thresholds.

Subject D

Position	1	2	3	4	5	6	7	8	9	10
Left (m. l. a.)	50.7	49.1	54.3	58.1	52.9	52.9	62.5	52.6	54.3	60.5
Left (m. l. a.)	54.9	53.8	54.1	57.5	60.6	63.7	72.1	68.7	59.4	61.2
Left (b. l. a.)	50.9	46.4	53.8	55.9	54.3	56.8	58.6	61.2	69.3	65.3
Right (m. l. a.)	53.6	58.5	56.4	50.8	49.7	59.0	53.9	58.5	55.3	58.5
Av.	52.5	52.0	54.6	55.5	54.4	58.1	61.7	60.2	59.6	61.4

Subject W

Position	1	2	3	4	5	6	7	8	9	10
Left (m. l. a.)	68.0	63.2	59.3	54.8	55.7	56.6	49.8	57.3	53.4	58.0
Left (m. l. a.)	63.0	60.3	56.9	59.8	60.7	58.8	55.6	55.3	59.1	56.3
Left (b. l. a.)	53.2	58.3	45.5	66.8	54.3	54.6	59.5	50.0	50.0	46.4
Right (m. l. a.)	58.5	61.2	61.2	60.5	57.3	64.7	61.6	52.2	61.2	54.4
Binocular	59.8	66.3	44.6	46.3	41.1	44.0	48.3	52.6	45.2	42.4
Av.	60.5	61.8	53.5	57.6	53.8	55.7	55.0	53.4	53.8	51.5

A somewhat similar analysis of the 1 min. light adaptation; 10 min. dark adaptation work in Part B shows the same trends in a less marked degree. Thresholds taken in successive periods are slightly higher for D and lower for W. For the 3 min. light adaptation followed by 15 min. dark adaptation there is no constant difference between successive periods for either subject.

E. *Summary of Experimental Results*

Foveal dark adaptation with right eye, left eye, and binocular observation was investigated for an interval of 10 min. (4 subjects) and 15 min. (5 subjects) after the cessation of light adaptation. A more intensive study was made (2 subjects) of the first 30 sec. of dark adaptation. Four subjects were tested monocularly during 1 hour's dark adaptation.

RESULTS

(1) For 3 subjects the average monocular thresholds after binocular light adaptation were about 50 per cent higher than the binocular thresholds. Differences between left and right eye thresholds were comparatively slight. Two of the 3 subjects in this group worked in all variations of the experiment.

(2) For 3 subjects the binocular thresholds approximated those of the more sensitive eye.

(3) Monocular thresholds were lower after binocular light adaptation than after monocular light adaptation. The difference was most marked at the beginning of dark adaptation, and was no longer present after 4 to 10 min. in darkness.

(4) Light adaptation for 3 min. gave decidedly higher succeeding thresholds than 1 min. light adaptation.

(5) Foveal dark adaptation was rapid for the first 30 sec. and slower thereafter. The " steepness " of the first part of the curve depends to a great extent on the arbitrary relation of the units of time and intensity used in plotting.

(6) With 3 subjects foveal dark adaptation continued for 50 to 60 min. after 3 min. light adaptation, with 1 subject for 20 to 25 min. This is based on a relatively small amount of monocular data.

With the exception of the form of the curve of foveal dark adaptation, which was determined by Hecht for extreme red light, all the work summarized above is novel. Binocular and monocular foveal relations had not been tested previously during the temporal course of dark adaptation.

V

Theoretical

A. *Foveal Dark Adaptation*

The results of previous work on foveal dark adaptation, as well as our own data, have shown that the sensitivity at the retinal center increases rapidly at first and then more gradually. It should be pointed out, however, that the exact form of the dark adaptation curve depends in a large measure on the method of plotting. Three methods have been used, one of which has its chief exponent in Hecht (23). By this the threshold intensities are plotted directly against the time of dark adaptation. The resulting graphs have the advantage of being simple and clear and thus easy to understand, and the additional merit of directly representing the experimental data. For these reasons Hecht's method is used throughout this paper.

Piper (40) and most early experimenters followed another method, by which the reciprocals of the threshold intensities (multiplied by a suitable constant) are plotted against dark adaptation time. To the writer Hecht's criticisms (23) of this procedure seem well founded. There is no good reason to suppose that the reciprocals of the thresholds directly measure retinal sensitivity, as Piper thought. The shape of his curves is largely due to the peculiar mathematical properties of a series of reciprocals.

The third method has been used by Best (11). It consists in taking the reciprocal of the *initial* dark adaptation threshold as the zero point of the curve and the ordinate units as powers of 2 ($2^1, 2^2, 2^3, 2^4....$). The sensitivity increase is thus considered as a geometrical rather than an arithmetical progression. Since the differences between the logarithms of successive powers of 2 are equal, any intermediate point can be plotted by taking the log. of the threshold reciprocal and interpolating between the

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logarithms of the next highest and next lowest power of 2. The three methods may be illustrated by 4 hypothetical thresholds taken after 1, 2, 3, and 4 min. dark adaptation and equalling 8, 4, 2, and 1 light units respectively. These would be treated by the three investigators as follows:

	Number of units on ordinate scale		
Actual thresholds	Hecht	Piper	Best
8	8	(⅛) 1	0 3
4	4	(¼) 2	1 or 2
2	2	(½) 4	2 1
1	1	(1) 8	3 0

A glance at the above table shows that Piper's mathematical treatment of the data completely reverses the rate of change for the first and last parts of the curve. The same data plotted by Hecht's method give the maximum change near the beginning, by Piper's the maximum change near the end of the curve. The general tendency of Best's treatment is to straighten the curve. In the above data it is a straight line. An advantage of Best's procedure is that, as far as the form of the curve is concerned, it makes no difference whether one starts from actual thresholds or their reciprocals. The right (second) set of units under Best's name in the table have threshold intensities as a basis, while the set on the left are reciprocals. While one gives a falling and the other a rising curve, the rate of change in the two is identical. Best's method is, however, too foreign to the usual procedure to be readily understood. For most purposes the simpler direct method seems best.

When foveal dark adaptation data are plotted by Hecht's method and the curve drops rapidly at first and then gradually slows down. The relation of early work to his own (on this point) has been discussed by Hecht and need not be elaborated here. In general our data agree with those of previous investigators as far as the general form of the foveal curve is concerned. A comparison of the curves for D and W with those given by Hecht reveals the same initial drop and later gradual descent. The curves for our other subjects have the same form, as could be determined from the few thresholds taken in the first minute of dark adaptation.

The thresholds taken in the first 30 sec. of dark adaptation, as reported in Part A of the " Experimental Data," are not strictly comparable with those taken after 30 sec. They differ in two ways: (1) The stimulus light was set constant in early thresholds, and moved toward the subject in later thresholds. (2) The current flowing through the lamp used to illuminate the fixation points was at one ampere for earlier thresholds and 0.8 ampere for later thresholds. This was probably not of much importance, as the subjective brightness was about the same in both cases. Moreover, the drop in the foveal curve during the first 30 sec. is so much greater than the drop after 30 sec. that it is unlikely that these two changes in procedure would cause any appreciable deviation from the true curve.

In still another sense the method of plotting influences the form of the curve. Hecht's data show a " precipitous " drop in the first few seconds. Yet similar data plotted on a different scale in Figs. 3 and 4 give curves with a smooth and gradual downward course. There is, however, no doubt of the continuous negative acceleration of the curve. Whether or not a sudden sharp bend appears is a function of the relative size and linear distance allotted to the units of time and intensity.

The increase in foveal sensitivity is somewhat greater for our subjects than for Hecht's—a difference probably due in part to individual differences and in part to the much greater intensity of light adaptation used in our work. Hecht's subjects, after their results are corrected for pupillary change, show an average increase in sensitivity of about 7 times between his first determination after 7 sec. and his final determination after 20 min. dark adaptation. In the present investigation the earliest threshold secured for W is the binocular at 5 sec., with a stimulus intensity of 840 light units (Table I). At the end of 10 min. this subject could just perceive a stimulus intensity of 44, one-nineteenth of the initial threshold. D's first thresholds were monocular at 5 sec., intensity 1082. Ten min. later this had been reduced to one-thirtieth, and at the end of 50 min. was less than 1 per cent of the first threshold intensity. Of the other subjects, A's threshold sensitivity increased 40 times from 4 sec.

to 1 hour, and T's threshold sensitivity increased 250 times from 6 sec. to 50 min., while the rest of our observers for 10 or 15 min. dark adaptation show a fairly close approximation to W's results.

B. *Binocular Summation*

Explanations of the greater binocular than monocular threshold sensitivity during dark adaptation found by many investigators * have been advanced by Piper, Lohmann, and Roelofs and Zeeman. The Duplicity Theory is the basis of Piper's view (40). He assumed that the cones are the organs of daylight vision, while the rods function only during dark adaptation. From his findings that summation only sets in after 10 to 15 min. dark adaptation he concluded that binocular summation is characteristic only of rod vision.

Lohmann's hypothesis (32) identifies summation with the well known dependence of dark adaptation threshold sensitivity on the area of the stimulus. From this he argued that a contra-position of non-identical monocular points would give an apparent summation by really widening the binocular field. His own words (33) are: ". . . bei binokulärer Reizung eine verschiedene Einstellung beider Augen die Ursache der Summierung sein könne. Eine Gegenüberstellung nicht identischer, aber jeweils im besonders begünstigtem Grade der Adaptation befindlicher Netzhautstellen gegenüber dem Reizlicht ergäbe nur scheinbar eine binokulare Summierung, in Wirklichkeit eine—binokulare!—Vergrösserung der Gesamtreizfläche." This is quite the opposite of Piper's view. According to the latter summation occurs only with exact correspondence of the retinal points, while the former makes it dependent on lack of such correspondence. Lohmann's argument, indeed, rests on a rather slender factual basis. Simon's observations (48) constitute the only evidence given that such a " Gegenüberstellung " of non-identical monocular points occurs in binocular vision. In any case, as Best (11) has pointed out, binocular summation and increase of monocular threshold sensitivity with the area of the

* See historical section.

stimulus follow different laws. Moreover, if Lohmann's theory held we would expect much greater binocular coöperation in cross-eyed persons than in normal subjects. This his own work (32) and Horn's experiments (27) with two squint-eyed subjects partially supported. A later and more extensive investigation by Stargardt (51), however, showed no difference between the frequency of summation in cross-eyed subjects and others.

Lohmann thought that his theory was supported by his discovery of greater summation with descending than with ascending thresholds (33). His line of argument was that stimuli appearing from below the threshold are reacted to almost as soon as seen. Descending threshold stimuli, on the other hand, are present in the visual field for a longer time and thus give more time for adjustive eye movements. These result in an increase of the stimulated area on the combined retinas.

For their explanation of summation Roelofs and Zeeman (45) draw on Hering's color theory. From Hering's assumption that light and darkness are both stimulating conditions, they argue that in monocular observation the darkness in the non-observing eye reduces the sensitivity of the stimulated eye. Binocular observation is thus the normal condition and in monocular observation darkness plays a positive inhibitory rôle. Lohmann (33) objects that, according to Hering, the sensation of the non-stimulated eye is a mean-grey which could not ("ohne weiteres!") reduce the sensation from the stimulated eye.

The main difficulty with Roelofs and Zeeman's theory as it stands, however, is that it explains too much. From it follows logically the summation of supra-threshold as well as threshold or sub-threshold brightness during dark adaptation. To explain why the former does not occur its authors advance the principle of "dominance of contours." This implies that the visual mechanism acts differently in perception of form and brightness. The lack of sharp contours at the threshold makes it easier for darkness in the one eye to reduce the sensitivity of the stimulated eye. Above the threshold the presence of a definite outline of

the object prevents the darkness from exerting any subjectively noticeable inhibitory effect.

Our experimental results, though partially explicable by Roelofs and Zeeman's theory, lend little positive support to any of the three theories mentioned. The existence of foveal summation is directly contrary to Piper's hypothesis that summation is a function of the rods but not of the cones. At least for the subjects who showed lower binocular than monocular thresholds the rod and cone apparatus cannot be differentiated on this basis. Summation is approximately as great immediately after light adaptation, when the cones presumably have maximum advantage over the rods, as at any later time. It is true that we only tested summation for 15 min. of dark adaptation, and Piper found little before this time. A partial support for his theory would be found if complete summation occurs in late dark adaptation. It must be remembered, however, that he was using large stimulus surfaces, and that with similar procedure Roelofs and Zeeman found approximately complete summation at the beginning of dark adaptation. Other observers found individual differences. Some of their subjects showed complete summation, some partial summation, and some none at all.

Lohmann's theory fares likewise when considered in the light of our results. There was certainly some eye-movement during the threshold observations, but there is no reason to suppose that it was greater binocularly than monocularly. Moreover, the careful centering of the stimulus and the efficiency of the fixation device ensured a close approximation to stimulation of identical points on the two retinas. If his theory were true, practice in holding fixation should decrease or eliminate summation. On the contrary, the summation effect appears consistently with the two most practiced subjects.

The Roelofs and Zeeman hypothesis fits in best with our data. The fact that monocular thresholds are lower after binocular than after monocular light adaptation receives a simple explanation if an inhibitory function is assigned to the darkness in the non-observing eye.

One difficulty for all theories of binocular summation is that

most experimenters have found individual differences in the existence and in the amounts of summation. This is true of our data. The source of such differences may be sought in innate characteristics of the visual mechanism or differences in developmental history. One possibility which arises is that binocular summation occurs in individuals whose eyes are about equal in sensitivity, but that when one eye is markedly more sensitive than the other the former dominates in binocular vision. Inspection of our data, however, fails to bear out this assumption. The results of former experimenters help little on the question, because few gave both monocular thresholds. Most seem to have taken limens for only one eye.

A second possible source of summation differences might lie in the method of observation. From the first consciousness of " something there " until the stimulus is clearly seen, a certain time elapses. It is possible that subjects differed in their criterion of " thereness." If the subjects who showed no summation were waiting until the outline of the object was clearly visible, their binocular-monocular equality might be explained by Roelofs and Zeeman's " dominance of contours." Unfortunately for the theory, the introspections from our subjects indicate no such constant difference between the method of observation used by the groups showing and not showing summation, respectively.

The neurological basis of summation probably lies in alliance (or interference) of impulses from corresponding points of the two retinas. As is well known, after the semi-decussation in the optic chiasma neurons from corresponding extrafoveal points of the two retinas run together and end in the external geniculate bodies or superior colliculi. Foveal fibers from both eyes, on the other hand, are about equally represented in the centers on both sides of the mid-brain. Piper (**40**), who first suggested the summation of monocular neural impulses in the mid-brain, also saw its difficulties for his theory that summation occurs with the rod mechanism, but not with the cones. There is no obvious reason why there should be a difference of this nature in the action of the neural impulses from rods and cones. If, as our results indi-

cate, summation can also occur with the cone mechanism, the difficulty disappears. In the next section reasons will be advanced for the belief that the complicated inhibitory-facilitatory relationships discovered by Allen, and the inhibition found by Heymans and Spencer, occur in the cortex. Binocular summation, however, may well have its seat in sub-cortical centers. The simple coöperation of pairs of corresponding points requires no complicated associative system and could take place in the mid-brain.

It might be mentioned that binocular summation is not closely allied with summation in nerve fibers following successive subthreshold stimuli. Binocular summation concerns the relations between simultaneous neural excitations. For further data the reader is referred to a summary and discussion by Cohen (17). Visual summation is more closely analogous to Sherrington's " Immediate spinal induction " (47). An example of the latter occurs in the scratch reflex of the spinal dog, where two simultaneous and spatially separated stimuli unite to arouse the reflex. Similar phenomena have been studied by Pavlov (39) and others.

C. *Effect on Monocular Thresholds of Preceding or Simultaneous Stimulation of the Other Eye*

It will be remembered that the data on the effect of stimulation of one eye on the dark adaptation thresholds of the other were somewhat conflicting. The three main theoretical contributions to this field do not offer a reconciliation of the conflict. The theories are Behr's hypothesis of sub-cortical regulatory centers, Heymans' law, and Allen's theory of " Reflex Visual Sensations." Piper's and Révész's negative findings call for no special interpretation.

Behr started with two of the postulates usually assumed by advocates of the " Duplicity " Theory.

(1) The rod and cone mechanisms function separately, the former being the apparatus for " twilight " vision, the latter for daylight vision.

(2) Increase in the sensitivity of the eye during dark adaptation is a result of the accumulation of visual purple in the rods.

The control of the accumulation of visual purple he assigned to sub-cerebral centers. From these centers run " Zentrifugalen die Sehpurpurbildung hervorrufenden und regelnden Fasern." The existence of such centers he deduced from clinical study of disturbances of dark adaptation sensitivity following lesions in the optic nerves and tract. From the semi-decussation of the optic nerves at the chiasma and subsequent juxtaposition of neurons from corresponding points of the two eyes, he argued that: " Strahlen nun diese so geordneten Stäbchenfasern in ein supponiertes subcerebrales Zentrum ein, so werden die von zwei identischen Netzhautpunkten kommenden Fasern entweder in eine oder in zweit in unmittelbarer Nachbarschaft nebeneinander gelegene Ganglienzellen einmunden. Haben diese dann weiter einen bestimmenden Einfluss auf die Regeneration des Sehpurpurs, so ist zu erwarten, dass durch eine gegenseitige Beeinflussung dieser Ganglienzellen die Belichtung eines Auges auf die gleichzeitige Dunkeladaptation des andern Auges einen hemmenden Einfluss ausübt."

However, Piper and Révész found no such effects. This is explained by reference to limitations in the functions of the regulative centers. They control the accumulation of visual purple, but have no power to destroy it when once accumulated. For the latter the direct action of light is necessary. Piper and Révész found no effect from stimulation of one eye on the dark adaptation of the other because they allowed the latter to adapt part of the time without any inhibitory influence. Behr himself found such effects because the inhibitory light stimulated the non-observing eye continuously *during the temporal course* of dark adaptation of the other eye.

The experiments of Heymans are based on theoretical considerations quite different from those of the investigators previously mentioned. Heymans postulated and tested the validity of the generalization known as " Heymans' Law," which states that: " The inhibitory power of a stimulus is proportional to its intensity." He, and Spencer, who later carried on the same line of investigation, were thus seeking to verify or disprove a general inhibitory function of all " secondary " stimuli. Piper,

Behr, and Révész, on the contrary, were concerned only with the effect of such secondary stimuli on the process of dark adaptation. As Spencer points out, the rôles of central inhibition and disturbance of dark adaptation in positive experimental results are exceedingly difficult to distinguish. The methods of Piper and Révész are indeed somewhat similar to those of Heymans and Spencer. Both involve the presentation of supra-threshold brightness to the non-observing eye and threshold stimuli to the observing eye. But in the Heymans-Spencer work the threshold taking and the presentation of the " inhibitory " stimulus are always simultaneous, while with Révész the two were sometimes simultaneous, sometimes successive. Negative findings involve no such analytic problem. The results of Piper oppose both the presence of central inhibition (or facilitation) and disturbance of dark adaptation.

Allen's theory of " Reflex Visual Sensations " agrees with Behr's hypothesis in assuming the existence of centrifugal fibers from sub-cortical or cortical centers to the two retinas. It differs from the latter in the wide scope of its application and the intricacy of the effects it attempts to explain. Behr's regulatory centers govern only the accumulation of visual purple. Allen's " reflex " nerve fibers condition the whole mechanism of vision. Every stimulus is supposed to produce a " direct " and a " reflex " effect. The direct effect is transmitted directly to the optic neurones by the visual receptors. " Reflex " effects, on the other hand, go to the brain and back again to the same and opposite retinas, where they reinforce or inhibit the direct effects.

It must be understood that the epoch-making nature of Allen's experiments * and their theoretical importance are not affected by the validity of this particular hypothesis. It seems to the writer, however, that the existence of " Reflex Visual Sensations " rests on a rather slender psycho-physiological basis. In the first place, although recent work supports the theory that centrifugal visual fibers exist, such a large number of neurones as the " reflex " theory requires could scarcely have escaped so long the attention of neurologists. Secondly, the reflex theory

* See Historical Section, also Parsons (38).

unduly complicates the visual reception and conduction system. Centripetal reflex and direct effects must be carried by different neurones or different processes in the same neurone. Since principles of nerve physiology, particularly the All or Nothing Law, make it difficult to find enough distinct neural processes to transmit the variables required by the simplest of the current visual theories, the burden of proof rests heavily on anyone venturesome enough to assign a new function to the already over-burdened visual conduction system.

Finally, neither Allen's data nor the findings of other experimenters require such a novel and intricate explanation. They can be understood by reference to less hypothetical anatomical relations and physiological laws. A careful reader of Allen's discussions can scarcely escape the conviction that the latter regards the retina as the seat of visual " sensations," and that he believes that interference and reinforcement must take place there. This is almost certainly not the case. What the observer perceives is not the stimulation of the receptors, but the conscious process. Inhibition and facilitation may take place at any centers in the optic pathway. Two such centers exist within each retina and another in the external geniculate bodies. The former permit reciprocal influence of excitations from points in the same retina. Alliance or interference of neural impulses from the two retinas can occur either in the external geniculate bodies or in the occipital cortex.

As regards the difference between " reflex " and " direct " effects the simplest explanation comes from the time-relations of the stimuli. Allen's inhibitory or facilitatory stimuli always preceded the taking of the thresholds. What he calls the " reflex " effect may be caused by a residue at the cortical synapses from previous direct stimulation.

It seems that the most reasonable hypothesis is some form of central inhibition or facilitation. In accordance with Sherrington's theory, now generally accepted, this would take the form of alliance or interference of neural impulses impinging on a final common path. Allen's data on the influence of pre-stimulation of the same retinal area, of the other half of the same

retina, and of the opposite retina, on the flicker thresholds for red, green, and blue, seem to require an intricate system of association fibers such as exists only in the cortex.

The hypothesis of a central site of the interaction of neural impulses agrees with the Heymans-Spencer view of "*central* inhibition." The general data, however, do not follow the simple inhibitory relationship formulated in " Heymans' Law." Allen found both facilitation and inhibition, depending on the wavelength as well as intensity of the influencing light.

Our own findings of facilitation of monocular thresholds by preceding binocular light adaptation, agree better with Allen's results than with those of any other investigator. They have, however, no positive disagreement with any previous work. All previous experimenters except Spencer and Allen dealt with the extrafoveal regions rather than the fovea, and none except Behr took thresholds until after at least 10 minutes dark adaptation had elapsed. At that time the facilitatory effect has vanished with our subjects.

On the whole, the most plausible interpretation is in line with a suggestion of Spencer's, that presentation of supra-threshold light inhibits simultaneous thresholds, but may either inhibit or facilitate thresholds taken after the supra-threshold light has ceased. Such an hypothesis would explain the inhibition found by Heymans, Spencer, and Behr, since all three used simultaneous stimulation of the non-observing eye, and still not conflict with the facilitation and inhibition found by Allen and the facilitatory results in our work, since with both Allen and ourselves the supra-threshold stimuli always preceded the threshold judgments. The only experimental data directly opposed to such a solution is that of Révész, and a few observations by Behr, who varied his usual " simultaneous " procedure by occasionally taking a monocular threshold with the non-observing eye in darkness.

The need for Behr's hypothesis of sub-cortical regulatory centers controlling the accumulation of visual purple depends on the decision of the conflict between the negative results of Révész and the Heymans-Spencer data. If, as their experiments

seem to prove, the Heymans-Spencer law that "the inhibitory power of a stimulus is proportional to its intensity," holds for the effect of simultaneous stimulation of one eye on the thresholds of the other, there is no need of a special hypothesis to cover the type of inhibition found by Behr. On the other hand, if later work should support Révész's conclusions, some additional mechanism must be postulated to explain Behr's results, and his own interpretation seems reasonable and satisfactory.

VI

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